PAPERS

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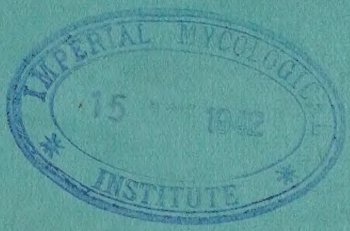
MICHIGAN ACADEMY OF SCIENCE ARTS AND LETTERS

XXVII (1941)

PART I: BOTANY AND FORESTRY



MICHIGAN ACADEMY OF SCIENCE ARTS AND LETTERS

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PART I: BOTANY AND FORESTRY

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PAPERS OF THE MICHIGAN ACADEMY OF SCIENCE ARTS AND LETTERS

EDITORS
EUGENE S. McCARTNEY
WILLIAM C. STEERE

VOLUME XXVII (1941)
PART I: BOTANY AND FORESTRY

"Pusilla res mundus est nisi in illo
quod quaerat omnis mundus habeat."
— SENECA, *Naturales Quaestiones*

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BOTANY

INHERITANCE OF TWO FACTORS AFFECTING ANTHOCYANIN DISTRIBUTION IN FLOWERS OF PETUNIA*

ERNEST E. DALE

IN THE course of inheritance studies in the garden petunia, *Petunia hybrida*, two factors have been isolated which affect the distribution of anthocyanin in the flowers. The first (Figs. 1–2) tends to inhibit the production of anthocyanin in the veins of the part of the corolla immediately adjacent to the throat margin. The second (Fig. 3) largely inhibits anthocyanin development in the outer limb of the corolla. The first type will be designated "pale-veined"; the second, "pale corolla."

TABLE I

SEGREGATION FOR PALE-VEINED FLOWERS IN PETUNIA

F_1 GENERATION

Family	Dark-veined	Pale-veined	Expected numbers	Standard error
1594	7	3		
1674	78	23		
1693	37	13		
Total	122	39	121 : 40	5.4
		Backcross		
1734*	49	50	49 : 50	5.0

* The reciprocal backcross failed to produce viable seed.

PALE-VEINED

The pale-veined type first appeared in a pink-flowered variegated strain of petunia which has been called "stippled" (unpublished).

* Papers from the Department of Botany and Botanical Gardens of the University of Michigan, No. 796.

Stippled flowers have a fine-speckled appearance, but this is hardly brought out in the photographs (Figs. 1–2). The character is unstable, and stippled plants often bear some normal flowers. In an inbred culture of ten pink-stippled plants three bore flowers in which the veins about the throat margin were *pale* (Fig. 1); the remaining seven bore dark-veined flowers (Fig. 2). To test the genetic constancy of *pale-veined* a progeny of eighty-two plants was grown from seed of selfed flowers. All were *pale-veined.* It seemed probable that *pale-veined* was a recessive monogenic character, and the data of Table I fully bear out this assumption.

TABLE II

SEGREGATION FOR NORMAL AND PALE COROLLA IN PETUNIA

F_2 GENERATION

Family	Normal	Pale corolla	Expected numbers	Standard error
1605	71*	20		
1608	7	1		
Total	78	21	74 : 25	4.1
Backcross				
1622	53	43		
1632	51	49		
Total	104	92	98 : 98	7.0

* Includes four light-colored plants.

PALE COROLLA

Malinowski (1914) and Rasmuson (1918) have described crosses involving a factor which appears to be genetically the same as the pale-corolla type reported here. Discussion of their work, however, will be deferred to a later part of the paper.

Newly opened flowers of the pale-corolla strain are a light purplish violet ("bishop's purple"; Ridgway). By the time the anthers dehisce the flowers normally become paler, being approximately "pale Hortense violet" (Ridgway), and eventually they may fade to nearly white. But fading is markedly affected by environmental factors, since plants grown in the greenhouse and blooming before the first of May showed only a slight change in flower color.

The inheritance of *pale-corolla* was studied in crosses with normal purple. Thirty-nine F_1 plants were obtained, and all were *normal*. The F_2 and the backcross data are given in Table II.

Four F_2 plants which bore light-colored flowers intermediate between typical *normal* and *pale corolla* have been classified as normal. It is known that F_1 hybrids of *pale corolla* × *white* and *pale corolla* × *pink* are purple. *Pale corolla*, therefore, carried the factor for purple. Since dark color (purple) is strongly inhibited in the presence of *pale corolla*, it seems likely that the light-colored plants referred to were not genetically *pale corolla*. But it is to be noted that, whether these plants are classed as *pale corolla* or *normal*, the data conform to expectation for recessive monogenic inheritance.

DISCUSSION

Malinowski (1914) obtained a ratio of 9 self-red : 3 red-veined : 4 self-white in F_2 of a cross between red-veined and a white-flowered variety of petunia. He assumed, in addition to a factor for color, a factor B "causing the distribution of color on the whole surface of the corolla; in the absence of the B factor . . . the only colored parts of the flower are the veins." It seems probable that Malinowski's B factor corresponds to the pale-corolla factor discussed in the present paper, but that *pale corolla* produces more pigment.

The study by Rasmuson (1918), which appears to involve the pale-corolla factor, concerned a cross between a variety of petunia with near-white flowers and a purple-flowered type. In F_2 he obtained 282 dark-colored : 98 light-colored plants. He found a high degree of variability among his light-colored F_2 segregates, but lumped them together as one genetic type. If the present writer's interpretation of the intermediate light-colored F_2 plants in Table II is correct, Rasmuson's procedure presumably involves some error. As was to be expected, no such intermediate types occurred in the backcross (Table II).

Pale-veined, as already stated, was found associated with a pink variegated strain of petunia which has been called "stippled." Like many other variegations, stippled plants occasionally produce some normal flowers, and an examination of these reverted normal flowers on pale-veined plants showed that the veins were fully colored. In sixteen pale-veined plants which bore some normal flowers the reverted normal flowers were in all cases *dark-veined*. In addition to

bearing occasional normal flowers, stippled plants sometimes produce chimeras, which combine sectors of normal and stippled tissue in one flower. Two such chimeral flowers were found, and in both the reverted normal sectors were *dark-veined*, whereas in the stippled areas the veins were pale. Thus the pale-veined factor produces no visible effect in the normal flowers of the stippled strain, but inhibits the production of color in the veins about the throat margin of the flowers when associated with "stippled."

Since "stippled" is recessive to *normal* and *pale-veined* is recessive to *dark-veined*, it appears that *pale-veined* may be determined by two pairs of complementary recessive genes. Critical tests of this hypothesis are being carried out.

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Schenectady, New York

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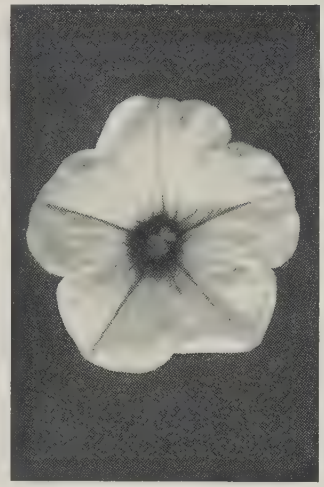


FIG. 1, *pale-veined*

FIG. 2, *dark-veined*

FIG. 3, *pale corolla*

Petunia flower types. All × 1

NOTES ON CAULERPA FROM JAVA AND THE PHILIPPINES *

WILLIAM J. GILBERT

IN THE course of graduate work at the University of Michigan the writer has had available for study the Chlorophyceae of several large algal collections from the region of Java and the Philippines. The Javanese collection was made under the direction of Dr. A. J. Kostermans, with the coöperation of the Laboratorium voor Onderzoek der Zee, Batavia, in the months of September and October, 1938. The material was preserved in formalin and sent to the University of Michigan in a score of five-gallon tins, where it was sorted and mounted and where collection numbers were assigned. In all there are 18 collecting localities, chiefly islands in the Bay of Batavia and in the Thousand Islands to the north; a few scattered stations range westward and south to Oedjoengkoelon, the western cape of Java. Two lots were gathered from the southern coast of Sumatra.

During the year 1935 Professor H. H. Bartlett, chairman of the Department of Botany, University of Michigan, was acting as an exchange professor at the University of the Philippines, Manila. While there he made a large collection of marine algae from all parts of the islands, which was given to the University of Michigan for identification and distribution. This collection includes a few specimens contributed by various students working with him at that time.

Furthermore, the New York Botanical Garden has loaned the writer its Philippine Chlorophyceae, most of which have never been reported upon and which consist largely of collections made in 1911 and 1913 by Dr. E. D. Merrill, Dr. W. R. Shaw, and others. There are also miscellaneous specimens and a few which were gathered by naturalists of the United States Fish Commission attached to the S.S. *Albatross* on an expedition conducted during the years 1907–10.

* Papers from the Department of Botany of the University of Michigan, No. 782.

So far as the writer is aware, the exact locality in the Philippines where the *Albatross* collections were made, and the month of year, are not known.

Abundant in this material is the genus Caulerpa, comprising more than 120 collection numbers and including a total of twelve species, with numerous varieties and forms. In his study the writer has been so impressed with the degree of variation of size and structure in certain of the species and with the number of transition forms from one species to another where there are many collections that he feels the line delimiting certain species of Caulerpa may be purely arbitrary. The absence of practically all field data, and also of preserved material for all but the Javanese collection, has been a real handicap in the satisfactory analysis of the plants at hand, since field data is especially vital in dealing with a polymorphic genus such as Caulerpa.

The marine flora of the region of the Netherland East Indies is already fairly well known through the monumental work for that area, Mme A. Weber–van Bosse's *Liste des algues du Siboga* (1913–28).

The Philippine algal flora, on the other hand, is comparatively unknown. Fewer than a dozen articles mention any Chlorophyceae, and these are all short lists, with the exception of the papers by Martens (1866) and Dickie (1876), which, though still lists, enumerate approximately seventy-five and fifty species respectively. In addition, the work of Mme Weber–van Bosse mentioned above covers the Sulu Archipelago, where a considerable number of Professor Bartlett's Philippine collections were made.

Ten of the twelve species reported in the present paper were found in the Javanese collection, but all ten have previously been listed from the Netherland East Indies, along with a considerable number of others (see Weber–van Bosse, 1913, pp. 96–114). Ten species (including those from the Sulu Archipelago) are here recorded from the Philippines, four of them (*Caulerpa fastigiata, C. parvifolia, C. cupressoides,* and *C. lentillifera*) newly listed for the islands. This brings to eleven the total number of species of Caulerpa known from the Philippines, with *C. selago* reported from the Sulu Archipelago but not found in the present material.

Following are the species, varieties, and forms represented in the several collections. Many call for no descriptive note, but in the more variable species some attention has been given to varietal and form differences.

List of Species

CAULERPA Lamouroux, 1809

1. *Caulerpa fastigiata* Montagne

References. — Montagne, 1838, p. 19, pl. 2, fig. 3; Weber–van Bosse, 1898, p. 262, pl. 20, figs. 1–2; 1913, p. 96; Børgesen, 1913, p. 118, fig. 93; Okamura, 1916, 4 (1) : 14, pl. 154, figs. 9–13; Taylor, 1928, p. 98, pl. 12, fig. 12.

Distribution. — Widely distributed in tropical waters.

Collections. — Philippines: *Villaflores 48*, Lubang Island, Mindoro Province, Sept. Java: *Kostermans 194*, Kaliage, Thousand Islands, Oct.

2. *Caulerpa verticillata* J. Agardh

References. — Agardh, J., 1847, p. 6; 1872, p. 6; Weber–van Bosse, 1898, p. 267, pl. 20, figs. 7–10; 1913, p. 96; Svedelius, 1906, p. 108, fig. 1; Børgesen, 1907, p. 355, fig. 1; 1913, p. 121, figs. 95–96; Taylor, 1928, p. 103, pl. 12, fig. 7, pl. 13, fig. 2; Yamada, 1934, p. 62, figs. 31–32; Tseng, 1936a, p. 175.

Distribution. — Widely distributed in tropical waters.

Collection. — Java: *Kostermans 610*, Anjer, west coast of Java, Oct.

3. *Caulerpa brachypus* Harvey

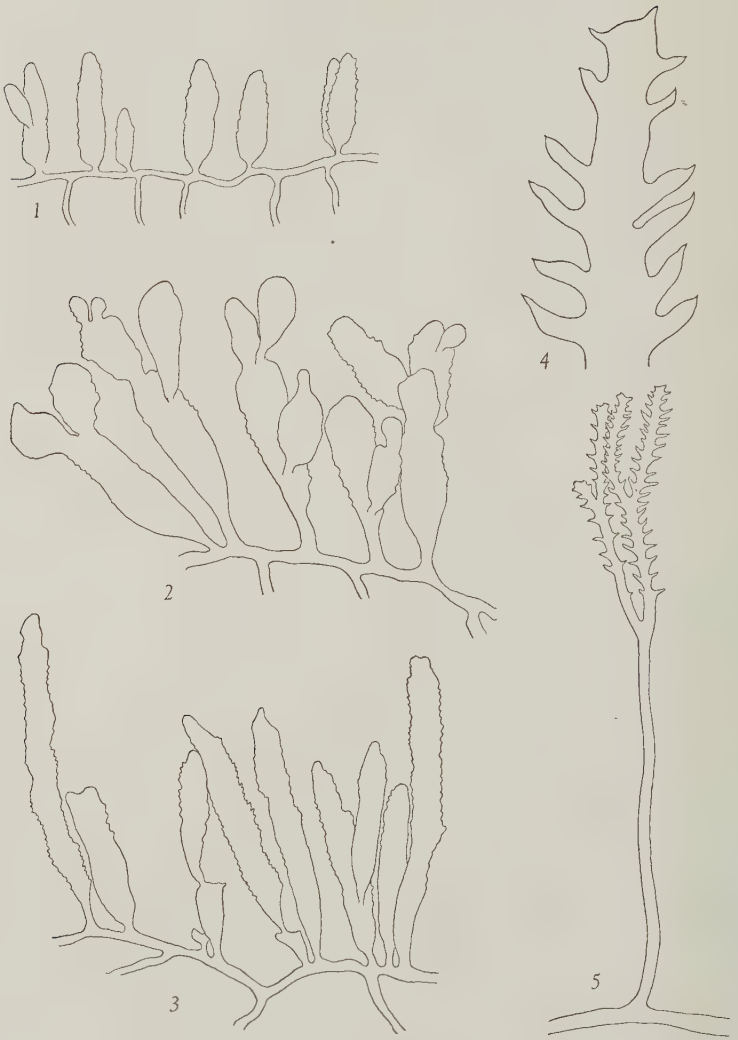
(Figures 1–3, p. 10)

References. — Harvey, 1859, p. 333; Agardh, J., 1872, p. 11; Kjellman, 1897, p. 33; Weber–van Bosse, 1898, p. 280, pl. 22, fig. 2; 1913, p. 97; Yamada, 1934, p. 65. *Caulerpa anceps* Harvey, Alg. exc. Fr. Isl., n. 67; Agardh, J., 1872, p. 9; Weber–van Bosse, 1898, p. 281, pl. 22, figs. 6–10; Yendo, 1903, p. 153; Okamura, 1914, 3 (5) : 94, pl. 125, figs. 1–8; Segawa, 1935, p. 62. *C. Stahlii* Weber–van Bosse, 1898, p. 282, pl. 22, figs. 3–4.

Distribution. — Japan, Polynesia, Malay Archipelago.

Collections. — Java: *Kostermans 189*, Kaliage, Thousand Islands, Oct.; *261*, Eil. Kelapa, Thousand Islands, Oct.; *321*, Poeloe Tjina, Thousand Islands, Oct.

The three collections from the region of Java include specimens which show this to be an extremely variable species. In the material at hand lie forms which could easily have fallen into *Caulerpa anceps*



Figs. 1–3. *Caulerpa brachypus*, showing variation in form. Figures 2–3 illustrate forms originally thought to be *C. Stahlii* and *C. anceps*, respectively. All × 1

Figs. 4–5. *Caulerpa serrulata* var. *Boryana* f. *longifolia*, f. nov. Fig. 4, detail of upper part of one frond, × 10. Fig. 5, habit, × 1.5

Harvey and *C. Stahlii* Weber–van Bosse if Yendo (1903, p. 153) had not shown them to be only growth forms of *C. brachypus*. Yendo suggests that the different forms are related to the season of the year in which the plant is found, but this is to be questioned, inasmuch as in the present collections, all of which were gathered within a period of two consecutive days, all the different forms are to be observed (Figs. 1–3). Rather, either the age of the plant or its immediate habitat is the likely determining factor affecting its form. Unfortunately, a description of the habitats in which the Javanese specimens were found is not available.

In several ways *Caulerpa brachypus* resembles *C. prolifera* Forsskål, and it is interesting to note that in the present material several of the fronds have margins which are entire except for a few small serrations, thus suggesting *C. prolifera* even more. On the same stolon, however, are fronds with delicate serrations around the entire edges, which, along with the fact that the fronds are also subsessile, indicates that the plant is not this species. From the Indo-Pacific region *C. prolifera* has been reported but once, by Weber–van Bosse (1913, p. 97), from Tanah Djampeah. Since at that time she called attention to the serrate character of a portion of the margin of one frond, it would seem that her specimen may well have been *C. brachypus*. The fact that Weber-van Bosse herself doubted the accuracy of her determination would tend to confirm the opinion that this report of *C. prolifera* in the Indo-Pacific region is questionable and that the plant with which she dealt may have been, as even she proposed, a large form of *C. brachypus*. The fronds of *C. prolifera* may have an undulate or, as generally, an entire margin, but are never spoken of as having teeth or as being serrate.

4. *Caulerpa parvifolia* Harvey

References. — Harvey, 1860, pl. 172; Agardh, J., 1872, p. 10; Weber–van Bosse, 1898, p. 281, pl. 22, fig. 5; 1913, p. 98; Okamura, 1930, p. 105; 1931, 6 (6) : 58, pl. 280, fig. 1; Yamada, 1934, p. 66, fig. 35; Tseng, 1936a, p. 176, fig. 29.

Distribution. — Japan, China Sea, Malay Archipelago, Australia.

Collection. — Philippines: *Bartlett 14993*, Dalupiri Island, Babuyan Group, Nov.

The largest frond is 11 mm. long; the usual length is 3–6 mm., and the width, 2–3 mm.

5. *Caulerpa crassifolia* (C. Agardh) J. Agardh

References. — *Caulerpa taxifolia β crassifolia* C. Agardh, 1822, p. 436. *C. crassifolia* (C. Agardh) J. Agardh, 1872, p. 13; Svedelius, 1906, p. 109; Vickers, 1908, pl. 40; Weber-van Bosse, 1913, p. 99; Børgesen, 1913, p. 130, figs. 102–103; 1939, p. 74; Taylor, 1928, p. 96. *C. pinnata* (L.) Weber–van Bosse, 1898, p. 289.

Distribution. — Polynesia, Malay Archipelago, Indian Ocean, Red Sea, Canary Islands, Caribbean.

Collection. — PHILIPPINES: *Albatross Expedition 34.*

Only a small plant was collected; most of its ramuli are rounded at the tip rather than mucronate. It is f. *typica* (Weber–van Bosse) Børgesen (1913, p. 131).

6. *Caulerpa taxifolia* (Vahl) C. Agardh

References. — *Fucus taxifolius* Vahl, 1802, p. 36. *Caulerpa taxifolia* (Vahl) C. Agardh, 1822, p. 435; Harvey, 1860, pl. 178; Weber–van Bosse, 1898, p. 292; 1913, p. 100; Svedelius, 1906, p. 112; Børgesen, 1907, p. 563; 1913, p. 131, figs. 104–105; 1932a, p. 58; Vickers, 1908, pl. 41; Okamura, 1913, 3 (2) : 38, pl. 110, figs. 4–5; Yamada, 1934, p. 67; Tseng, 1936a, p. 180.

Distribution. — Japan, China Sea, Philippines, Polynesia, Malay Archipelago, Indian Ocean, Caribbean.

Collections. — PHILIPPINES: *Bartlett 16128*, North Ubian Island, Sulu Archipelago, Sept. JAVA: *Kostermans 263a*, Eil. Kelapa, Thousand Islands, Oct.; *467c*, Poeloe Pajoeng, Oct.; *611a*, Anjer, west coat of Java, Oct.

7. *Caulerpa sertularioides* (Gmelin) Howe

References. — *Fucus sertularioides* Gmelin, 1768, p. 154, pl. 15, fig. 4. *F. plumaris* Forsskål, 1775, p. 190. *Caulerpa plumaris* (Forsskål) C. Agardh, 1822, p. 436; Kützing, 1849, p. 496; Dickie, 1876, p. 245; Weber–van Bosse, 1898, p. 294, pl. 24, figs. 4–6, 10. *C. sertularioides* (Gmelin) Howe, 1905, p. 576; Svedelius, 1906, p. 114, figs. 7–10; Børgesen, 1907, p. 365, fig. 11; 1913, p. 133, fig. 106; Vickers, 1908, pl. 42; Collins, 1909, p. 334; Weber–van Bosse, 1913, p. 100; Okamura, 1913, 3 (2) : 36, pl. 110, figs. 1–3; Yamada, 1934, p. 68; Tseng, 1936a, p. 179.

Distribution. — Widely distributed in tropical waters.

F. *brevipes* (J. Agardh) Svedelius

Reference. — Svedelius, 1906, p. 114.

Collections. — PHILIPPINES: *Bartlett 14021*, Manila Channel, Puerto Galera, Mindoro, 1935. JAVA: *Kostermans 51*, Eil. Hoorn, Bay of Batavia, Sept.

F. *longiseta* (Bory) Svedelius [perperam *C. sertularioides* f. *longiseta* (J. Agardh) Svedelius]

Reference. — Svedelius, 1906, p. 114.

Collections. — PHILIPPINES: *Bartlett 13940*, Puerto Galera Bay, Puerto Galera, Mindoro, May; *15579*, small island opposite Culion Harbor, Culion Island, Calamian Group, July. *Merrill 9144*, Taytay, Palawan, April. *Shaw 1130*, Cabcaban, Bataan Province, Luzon, May. JAVA: *Kostermans 184*, Kaliage, Thousand Islands, Oct.; *264*, Eil. Kelapa, Thousand Islands, Oct.; *324*, Poeloe Tjina, Thousand Islands, Oct.; *467a* and ?*467b*, Poeloe Pajoeng, Oct.; ?*586*, Poeloe Toenda (P. Babi), Oct.; *611b*, Anjer, west coast of Java, Oct.

In the literature there is considerable confusion regarding the limits of f. *longiseta*, but this seems unwarranted in view of the fact that the original description of *Caulerpe plumaire* var. β *Longiseta* Bory (1826, pp. 193–194, pl. 22, fig. 4) seems quite definite. Bory used the term to apply to plants of this species that are soft and that have fronds which are nearly always simple and borne singly, which are sessile or very briefly pedicellate, and which are 2.0–3.5 inches high, with ramuli 0.45–0.78 or even 1.0 cm. long.

The plants from Java and the Philippines under this form seem to fall into two general groups, the aspect of which is much the same, but which differ in size of frond, length of ramuli, and closeness with which the ramuli are arranged. The first group, including most of the Javanese plants, are of the smaller type, in which the ramuli are about 15 to a centimeter and 0.5–0.7 cm. long, and in which the fronds reach a height of 4.0 cm. and have a very soft appearance. Svedelius (1906, p. 114, figs. 7–10) has illustrated this group.

Bartlett 15579 and *Merrill 9144*, from the Philippines, represent the second group, in which the ramuli are 10–11 to a centimeter and up to 1.0 cm. long, and in which the fronds may reach a height of 9.0 cm. and in general appearance are coarser than those of the plants

mentioned previously. Branching rarely occurs in either group. *Shaw 1130*, from the Philippines, clearly represents a transition between these two general types, and it would seem that the larger ones are typical either of older plants or plants growing in more favorable habitats or both.

Caulerpa sertularioides (Gmelin) Howe f. *longiseta* (Bory) Svedelius has in the past been incorrectly cited as *C. sertularioides* f. *longiseta* (J. Agardh) Svedelius, but the term *longiseta* was first used by Bory (1826, p. 194) for var. *β Longiseta* under *Caulerpe plumaire*, a synonym of *Caulerpa sertularioides*.

Provisionally assigned here are *Bartlett 13940*, *Kostermans 467b*, and *Kostermans 586*, which resemble f. *longiseta* more than they do any other form, but in which the ramuli are relatively wider and the fronds show the interrupted character usually ascribed to periodic growth.

8. *Caulerpa serrulata* (Forsskål) J. Agardh emend. Børgesen

References. — *Fucus serrulatus* Forsskål, 1775, p. 189. *Caulerpa Freycinetii* C. Agardh, 1822, p. 446; Weber–van Bosse, 1898, p. 310, pl. 25, figs. 4–11, pl. 26, figs. 1–6; 1913, p. 102; Svedelius, 1906, p. 115; Okamura, 1913, 3 (1) : 18, pl. 105, figs. 1–6. *C. serrulata* J. Agardh, 1836, p. 174 (not seen, quoted from Weber–van Bosse, 1898, p. 311). *C. serrulata* (Forsskål) J. Agardh emend. Børgesen, 1932b, p. 5; 1940, p. 50; Tseng, 1936a, p. 178, fig. 31.

Distribution. — Widely distributed in Indian and tropical Pacific waters.

This species is well represented in the collections, with two varieties and several different forms, listed below. In addition, two specimens from Java (*Kostermans 179*, Kaliage, Thousand Islands, Oct.; *323*, Poeloe Tjina, Thousand Islands, Oct.) were too fragmentary to assign to any particular variety. The frequency of its occurrence in the Philippine material makes it surprising that the species has previously been recorded but a single time for the islands (Weber–van Bosse, 1913, p. 102).

Var. *typica* (Weber–van Bosse) Tseng

Reference. — Tseng, 1936a, p. 178.

F. *lata* (Weber–van Bosse) Tseng

Reference. — Tseng, 1936a, p. 178, fig. 31.

Collections. — PHILIPPINES: *Santos 128*, Wawa, Nasugbu, Batangas Province, July. *Bartlett 13937*, Puerto Galera Bay, Puerto Galera, Mindoro, May; *14971*, Currimao, Ilocos Norte Province, Luzon, Oct.; *15593a*, small island opposite Culion Harbor, Culion Island, Calamian Group, July; *16145*, Little Santa Cruz Island, Basilan Strait, southwest of Zamboanga, Mindanao, Sept.; *16174*, Mactan Island, opposite Cebu, Cebu Island, Sept. *Merrill 9155*, Taytay, Palawan, April. *McGregor, Bureau of Science 18480*, Biliran, June. *Hallier 588*, Zamboanga, Mindanao, Feb. JAVA: *Kostermans 12*, Eil. Kerkhof, Bay of Batavia, Sept.; *79*, Eil. Leiden, Bay of Batavia, Sept.; *265*, Eil. Kelapa, Thousand Islands, Oct.; *413*, Eil. Amsterdam, near Bay of Batavia, Oct.; *469*, Poeloe Pajoeng, Oct.; *612*, Anjer, west coat of Java, Oct.

F. **serrulata** (Forsskål), comb. nov.

Reference. — *Caulerpa Freycinetii* var. *typica* f. *serrulata* Weber–van Bosse, 1898, p. 314.

Collections. — PHILIPPINES: *Merrill 9142*, Taytay, Palawan, April. JAVA: *Kostermans 50*, Eil. Hoorn, Bay of Batavia, Sept.

F. **spiralis** (Weber–van Bosse), comb. nov.

Reference. — *Caulerpa Freycinetii* var. *typica* f. *spiralis* Weber–van Bosse, 1898, p. 314.

Collections. — JAVA: *Kostermans 49*, Eil. Hoorn, Bay of Batavia, Sept.; *112*, Eil. Edam, Bay of Batavia, Sept.; *587*, Poeloe Toenda (P. Babi), Oct.

Var. **Boryana** (J. Agardh), comb. nov.

References. — *Caulerpa Boryana* J. Agardh, 1872, p. 20. *C. Freycinetii* var. *de Boryana* Weber–van Bosse, 1898, p. 315.

F. **occidentalis** (Weber–van Bosse), comb. nov.

Reference. — *Caulerpa Freycinetii* var. *de Boryana* f. *occidentalis* Weber–van Bosse, 1898, p. 315.

Collections. — PHILIPPINES: *Bartlett 15577*, small island opposite Culion Harbor, Culion Island, Calamian Group, July; *16032b*, Siasi Island, Sulu Archipelago, Sept.

F. **longifolia,** f. nov.

(Figures 4–5, p. 10)

Dentes tam longi quam latitudo rhachium.

Collection. — Philippines: *Bartlett 16032a,* type, Siasi Island, Sulu Archipelago, Sept.

This new form of var. *Boryana* exhibits the characteristics of the variety, with the fronds having a long cylindrical pedicel and a flat linear blade, which is only slightly twisted, but it differs from other forms in the size and shape of the teeth, which are opposite to subopposite, somewhat spreading, reach a length equal to the width of the frond between the teeth bases, and are narrowed more or less sharply toward their pointed or mucronate tips. The teeth of all other forms of var. *Boryana* are wider at their base than high. One of the fronds has teeth borne tristichously for a short distance, but this arrangement, though of rare occurrence, has already been shown in the species (Weber–van Bosse, 1898, p. 316).

9. *Caulerpa cupressoides* (Vahl) C. Agardh

References. — *Fucus cupressoides* Vahl, 1802, p. 29. *Caulerpa cupressoides* (Vahl) C. Agardh, 1822, p. 441; Agardh, J., 1872, p. 21; Weber-van Bosse, 1898, p. 323, pl. 27, figs. 1–14, pl. 28, figs. 1–12; 1913, p. 103; Svedelius, 1906, p. 115; Børgesen, 1913, p. 135, figs. 108–116; 1940, p. 50; Okamura, 1916, 4 (1): 16, pl. 155, figs. 1–3; Taylor, 1928, p. 96, pl. 12, figs. 18–19, pl. 13, figs. 4, 16; Tseng, 1936a, p. 177, fig. 30.

Distribution. — Widely distributed in tropical waters.

Var. *typica* Weber–van Bosse

Reference. — Weber–van Bosse, 1898, p. 327.

Collection. — Java: *Kostermans 721,* Lampoeng Bay, Sumatra, Oct.

Var. *Lycopodium* (J. Agardh) Weber–van Bosse

Reference. — Weber–van Bosse, 1898, p. 335.

F. *alternifolia* (Crouan) Weber–van Bosse

Reference. — Weber–van Bosse, 1898, p. 336.

Collection. — Java: *Kostermans 466,* Poeloe Pajoeng, Oct.

F. *elegans* (Crouan) Weber–van Bosse

Reference. — Weber–van Bosse, 1898, p. 336.

Collections. — Java: *Kostermans 183*, Kaliage, Thousand Islands, Oct.; *262*, *263b*, Eil. Kelapa, Thousand Islands, Oct.; *588*, Poeloe Toenda (P. Babi), Oct.

F. *amicorum* (Harvey) Weber–van Bosse

Reference. — Weber–van Bosse, 1898, p. 337.

Collection. — Philippines: *Bartlett 13781*, Puerto Galera Bay, vicinity of Puerto Galera, Mindoro, May.

This is the only specimen of *Caulerpa cupressoides* in the Philippine collection. The ramuli throughout the plant are distichous, with no indication of a tristichous or multiseriate arrangement, but the branches, with a few exceptions, are produced on a third plane, which is not unusual for the species. The conception of f. *amicorum* of Tseng (1936a, p. 177, fig. 30) and Okamura (1916, 4[1]:16) suggests very strongly the length, shape, and arrangement of the ramuli of the Philippine specimen, except that these authors report that the ramuli are at times tristichous, or even multiseriate.

?Var. *ericifolia* (Turner) Weber–van Bosse

Reference. — Weber–van Bosse, 1898, p. 335.

Collection. — Java: *Kostermans 609*, Anjer, west coast of Java, Oct.

The specimen is so small and fragmentary that it is assigned to this variety with hesitation; the ramuli, however, are multiseriate and cylindrical, and some of them lie closely appressed to the central axis of the frond, which are characters of the variety.

10. *Caulerpa racemosa* (Forsskål) J. Agardh

References. — *Fucus racemosus* Forsskål, 1775, p. 191. *Caulerpa racemosa* (Forsskål) J. Agardh, 1872, p. 35; Dickie, 1876, p. 244 (as *C. clavifera*); Weber–van Bosse, 1898, p. 357, pl. 31, figs. 5–8, pl. 32, figs. 1–7, pl. 33, figs. 1–23; 1913, p. 104, figs. 26–28; Børgesen, 1907, p. 378; Okamura, 1913, 3(4):66, pl. 119, figs. 1–5; 1931, 6(6):58, pl. 280, figs. 2–9; Taylor, 1928, p. 101, pl. 12, figs. 3, 5–6, 8, 14, pl. 13, figs. 3, 8–11; Yamada, 1934, p. 71; Tseng, 1936a, p. 180, fig. 32.

Distribution. — Widely distributed in tropical waters.

This species is abundant in the collections studied, but its very abundance made separation of the specimens into varieties and forms difficult, since the transition forms seem to be almost as numerous as the collections. The need for critical field notes was especially felt here.

Var. *microphysa* (Weber–van Bosse) Taylor

Reference. — Taylor, 1928, p. 102.

Collections. — Java: *Kostermans 468*, Poeloe Pajoeng, Oct.; *589*, Poeloe Toenda (P. Babi), Oct.

The fronds are 3–15 mm. in length and unbranched, the shorter ones with only three or four ramuli, the longer ones with many. The ramuli have a short pedicel, occasionally as much as 1 mm. long, which suddenly expands into a globular head 1.0–1.5 mm. in diameter. At times there is a suggestion of a constriction between the globular head and the pedicel of the ramulus, which may indicate some relationship between var. *microphysa* and the Pedicellatae of J. Agardh. However, neither of the two specimens shows the marked constriction characteristic of all the Pedicellatae, including *Caulerpa lentillifera*, which *C. racemosa* var. *microphysa* otherwise rather closely resembles.

Var. *clavifera* (Turner) Weber–van Bosse

Reference. — Weber–van Bosse, 1898, p. 361.

Collections. — Philippines: *Santos 129*, Wawa, Nasugbu, Batangas Province, July. *Bartlett 13942*, Puerto Galera Bay, vicinity of Puerto Galera, Mindoro, May; *14004*, Batangas Channel, Puerto Galera, Mindoro; *14976*, Dalupiri Island, Babuyan Group, Nov.; *15420*, Basco, Batan Island, Batanes Province, July; *16052*, Harbor of Jolo, Jolo Island, Sulu Archipelago, Sept.; *16144*, Little Santa Cruz Island, Basilan Strait, near Zamboanga, Mindanao, Sept. *Merrill 9139*, Taytay, Palawan, April; *9162*, Taytay, Palawan, May. *Shaw 1128*, *1129*, Cabcaban, Province of Bataan, Luzon, May. *Williams* (no collection number), on coral reef, Darong, Mindanao, March 21, 1905. *Fénix, Bureau of Science 13006*, Puroton Reef, San Fernando, La Union Province, Luzon, Dec. *Curran, Forestry Bureau 9560*, Piapi, Tayabas Province, Luzon, March. *Albatross Expedition 7*, *9*. Java: *Kostermans 5*, Eil. Kerkhof, Bay of Batavia, Sept.; *52*, Eil. Hoorn, Bay of Batavia, Sept.; *111*, Eil. Edam, Bay of Batavia,

Sept.; *266*, Eil. Kelapa, Thousand Islands, Oct.; *412*, Eil. Amsterdam, near Bay of Batavia, Oct.; *472*, Poeloe Pajoeng, Oct.

Included here are those specimens with fronds up to 3 cm. in length, the ramuli being more or less spaced and consisting of a lower portion, 0.5–1.0 mm. in length, which gradually expands into a rounded end, 2 3 mm. in diameter. In a few, particularly *Bartlett 13942*, some of the ramuli have rather longer pedicels and quite suddenly expand into the globular tip, thus suggesting var. *occidentalis;* but because the condition is not uniform throughout the whole plant and because the fronds are shorter than typical var. *occidentalis* the specimens are included here.

Var. *macrophysa* (Kützing) Taylor

Reference. — Taylor, 1928, p. 101.

Collections. — PHILIPPINES: *Bartlett 16126a, 16129*, North Ubian Island, Sulu Archipelago, Sept. JAVA: *Kostermans 4*, Eil. Kerkhof, Bay of Batavia, Sept.; *180, 182, 192*, Kaliage, Thousand Islands, Oct.; *267*, Eil. Kelapa, Thousand Islands, Oct.; *322*, Poeloe Tjina, Thousand Islands, Oct.; *613*, Anjer, west coast of Java, Oct.; *720*, Seboekoe, Lampoeng Bay, Sumatra, Oct.

The fronds reach 4 cm. in length. The ramuli expand rather suddenly into a spherical or, more rarely, a flattened end 3–5 mm. in diameter, and are from 3 mm. (or less) to 5 mm. apart.

It is interesting that the usual form of the ramuli tips is spherical rather than "depressed-convex," as Taylor (1928, p. 101) describes the Florida material. That the typical form is rounded there can be little doubt, for the figure of *Chauvinia macrophysa* Kützing (1857, pl. 15) from the coast of Central America, on which Weber–van Bosse based her f. *macrophysa* and Taylor based the variety, shows most of the ramuli spherical, with a few compressed; this is characteristic of the Javanese and Philippine material.

Okamura (1913, pl. 119, fig. 1) in illustrating his conception of *Caulerpa racemosa* var. *clavifera* f. *macrophysa* shows a plant with the ramuli having almost spherical ends, only an occasional one being depressed. His illustration is of a plant strikingly similar to several of the present collections.

What appears to be a transition form between varieties *macrophysa* and *laetevirens* is represented by *Kostermans 192; Bartlett 16126b* shows certain affinities to var. *occidentalis.*

Var. *macra* Weber–van Bosse

Reference. — Weber–van Bosse, 1913, p. 106, fig. 26.
Collections. — PHILIPPINES: *Bartlett 15576*, small island opposite Culion Harbor, Culion Island, Calamian Group, July. JAVA: *Kostermans 110*, Eil. Edam, Bay of Batavia, Sept.; *191*, Kaliage, Thousand Islands, Oct.; *268*, Eil. Kelapa, Thousand Islands, Oct.

Weber–van Bosse described this variety to accommodate a large and robust specimen of *Caulerpa racemosa*, which was found growing in very quiet water. The plants in the present collections reach the dimensions given for the variety, especially *Bartlett 15576*, which has a stolon up to 6 mm. in diameter and more than 40 cm. long and fronds 5–11 cm. in length. The ramuli are almost entirely pyriform, swelling sometimes abruptly, but more often gradually, from the base to the rounded tip. Some of the ramuli reach a length of a little more than a centimeter, are arranged alternately, and are not crowded.

It is quite impossible to ascertain whether the specimens listed above were found in quiet waters.

Var. *uvifera* (Turner) Weber–van Bosse

Reference. — Weber–van Bosse, 1898, p. 362.
Collection. — PHILIPPINES: *Albatross Expedition 38.*

The one specimen is largely characterized by the multiseriate and imbricate obovoid or obovoid-compressed ramuli of var. *uvifera*, but shows some affinity to var. *lactevirens*, since some of the ramuli are cylindrical or elongate-clavate.

Var. *corynephora* (Montagne) Weber–van Bosse

Reference. — Weber–van Bosse, 1898, p. 364.
Collections. — PHILIPPINES: *Albatross Expedition 8, 29.*

?Var. *occidentalis* (C. Agardh) Børgesen

Reference. — Børgesen, 1907, p. 379.
Collection. — JAVA: *Kostermans 80*, Eil. Leiden, Bay of Batavia, Sept.

It is with hesitation that this specimen is included here, but since the ramuli appear alternate and somewhat distichous, are not

crowded, and are suddenly swollen into a rounded tip from a fairly long pedicel, the plant seems to belong to this rather than to any other variety.

Var. *laetevirens* (Montagne) Weber–van Bosse

Reference. — Weber–van Bosse, 1898, p. 366.
Collections. — PHILIPPINES: *Albatross Expedition 64.* JAVA: *Kostermans 193,* Kaliage, Thousand Islands, Oct.; *269,* Eil. Kelapa, Thousand Islands, Oct.; *471,* Poeloe Pajoeng, Oct.

The Javanese specimens have fronds up to 5–6 cm. high, with the typical densely imbricate ramuli, which are gradually swollen to a rounded summit. The fronds of the Philippine specimen reach 13 cm. in height; the ramuli are elongate-cylindrical and as much as 1 cm. long.

Var. *Lamourouxii* (Turner) Weber–van Bosse

Reference. — Weber–van Bosse, 1898, p. 368.
Collections. — JAVA: *Kostermans 3,* Eil. Kerkhof, Bay of Batavia, Sept.; *81,* Eil. Leiden, Bay of Batavia, Sept.; *190,* Kaliage, Thousand Islands, Oct.; *411,* Eil. Amsterdam, near Bay of Batavia, Oct.; *590,* Poeloe Toenda (P. Babi), Oct.

All the specimens are f. *typica* Weber–van Bosse, and vary from plants with a complanate frond almost destitute of ramuli to ones with fronds consisting of an erect axis which is almost cylindrical and having numerous, but not crowded, distichous cylindrical or clavate ramuli.

Var. *gracilis* (Zanardini) Weber–van Bosse

Reference. — Weber–van Bosse, 1898, p. 370.
Collection. — PHILIPPINES: *Albatross Expedition 34.*

Var. *Chemnitzia* (Esper) Weber–van Bosse

Reference. — Weber–van Bosse, 1898, p. 370.
Collections. — JAVA: *Kostermans 325,* Poeloe Tjina, Thousand Islands, Oct.; *530,* Toppershoedje, an island between Strait Soenda and Java Sea, Oct.

The plants are rather delicate, with fronds up to 2 cm. in height. The ramuli are numerous and imbricate, trumpet-shaped, enlarging gradually from the base to the flattened top.

11. *Caulerpa peltata* Lamouroux

References. — Lamouroux, 1809, p. 145, pl. 3, fig. 2 (not seen, quoted from Weber–van Bosse, 1898, p. 373); Agardh, J., 1872, p. 37; Dickie, 1876, p. 244; Weber–van Bosse, 1898, p. 373, pl. 31, figs. 9–11, pl. 32, figs. 8–9; 1913, p. 110; Svedelius, 1906, p. 131; Børgesen, 1925, p. 112, fig. 47; 1932a, p. 62, fig. 5; Okamura, 1931, 6 (6) : 60, pl. 280, figs. 10–12; Yamada, 1934, p. 72; Tseng, 1936b, p. 176, fig. 4.

Distribution. — Widely distributed in tropical waters.

In this species have been included all those specimens with few to all peltate ramuli. Transition forms are found in the specimens listed under var. *typica;* they vary from plants in which all ramuli are peltate to ones in which only a few of the ramuli are typically peltate and the others range in shape to the clavate form of *Caulerpa racemosa* var. *clavifera,* the trumpet-like and imbricate ramuli of *C. racemosa* var. *Chemnitzia,* or the suddenly expanded spherical-tipped ramuli of *C. racemosa* var. *occidentalis.*

All these transition forms may at times be found on the same plant and largely even on the same frond. This serves to illustrate once again that the line distinguishing *Caulerpa peltata* from *C. racemosa* is apparently quite arbitrary. The writer feels, however, that it is best to retain them as separate species, although acknowledging the evidence which shows they may not be, until the degree of hybridization in the genus Caulerpa is better understood. Cultural investigation should prove a most valuable aid to systematic studies in this genus.

Var. *typica* Weber–van Bosse

Reference. — Weber–van Bosse, 1898, p. 375.

Collections. — Philippines: *Santos 127,* Wawa, Nasugbu, Batangas Province, July. *Bartlett 13943,* Puerto Galera Bay, Puerto Galera, Mindoro, May; *14975,* Dalupiri Island, Babuyan Group, Nov.; *16126b, 16127,* North Ubian Island, Sulu Archipelago, Sept. Java: *Kostermans 178,* Kaliage, Thousand Islands, Oct.; *470,* Poeloe Pajoeng, Oct.; *529, 531,* Toppershoedje, Oct.; *664,* Oedjoengkoelon, western cape of Java, Oct.; *718, 719,* Seboekoe, Lampoeng Bay, Sumatra, Oct.

The average diameter of the peltate tips is about 3 mm., which is typical for the variety, but in *Bartlett 16127* the diameter reaches 6 mm., almost the maximum for the variety.

Var. *macrodisca* (Decaisne) Weber–van Bosse

Reference. — Weber–van Bosse, 1898, p. 376.

Collection. — Java: *Kostermans 758*, Belimbing, on the south coast of Sumatra, Oct.

Only one specimen at hand represents this variety. The diameter of the peltate tips of some of the ramuli reaches 1.0 cm. The ramuli are comparatively few and widely spaced. Variety *macrodisca* has also been reported from the Philippines (Howe, 1932, p. 169), from Panay Island, under the name *Caulerpa macrodisca* Decaisne. This collection, which the writer has seen, has specimens with peltate ramuli which exceed 2 cm. in diameter.

12. *Caulerpa lentillifera* J. Agardh

References. — Agardh, J., 1836, p. 173 (not seen, quoted from De Toni 1889, 1: 483); 1872, p. 42; Weber–van Bosse, 1898, p. 380, pl. 34, figs. 1–2; 1913, p. 112. *Caulerpa longistipitata* (Weber–van Bosse) Svedelius, 1906, p. 137, figs. 45–46.

Distribution. — Japan, China Sea, Polynesia, Malay Archipelago, Indian Ocean, ? Caribbean.

Collections. — Philippines: *Bartlett 13941*, Puerto Galera Bay, Puerto Galera, Mindoro, May. Java: ? *Kostermans 181*, Kaliage, Thousand Islands, Oct.

The constriction of the ramulus pedicel characteristic of this and other species of the Pedicellatae, is not so evident in the Javanese plant, but the length of the frond, the long pedicels of the ramuli, and the constriction, though slight, would seem to indicate that it should be placed here, rather than in *Caulerpa racemosa* var. *microphysa*, to which it bears certain resemblances.

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NOTES ON THE ALGAL FLORA OF MICHIGAN *

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TAXONOMIC studies of the Michigan algae have been published at intervals since 1894 (19). Ackley (2) and Nichols and Ackley (17) compiled a list of 950 species, varieties, and forms found in the state. Investigation has been particularly active in the last decade, as is shown by the bibliography at the end of this paper and the fact that 1,433 species have now been listed. This is a greater number than is known from any other state.

Material for the study reported here was gathered in Charlevoix, Cheboygan, Emmet, Otsego, and Presque Isle counties. Twenty-one species (marked with asterisks in the list below) are new to the state; eighty-two are listed for a second time.

Table I is a census of the known algae, exclusive of the diatoms, arranged in taxonomic groups; it shows that certain groups have not been adequately studied and that most of the species have been reported but once. Records for the flagellated groups are especially scarce. Even the group best represented, the Desmidiaceae, which accounts for about 40 per cent of the total number of species, should have considerably more attention, as is indicated by the fact that nearly half of the known species have been reported since the publication of the summary paper by Nichols and Ackley (17) in 1932. Since more than 70 per cent of all known species have been recorded by only one observer there is obvious need of confirmatory data.

Present interest in the algae, coupled with the fact that some papers have been overlooked by previous investigators, warrants the inclusion of a complete bibliography of articles on the Michigan algae, exclusive of those concerned solely with diatoms.

* Thanks are due the Williams College 1900 Fund for financial assistance and the University of Michigan Biological Station for the privileges and courtesies extended during the course of the investigation.

TABLE 1

CENSUS OF ALGAE KNOWN FROM MICHIGAN, INCLUDING SPECIES, VARIETIES, AND FORMS, ARRANGED IN TAXONOMIC GROUPS

Group	Number previously reported				Number reported in this paper	
	Once	Twice	More than twice	Total	For the first time	For the second time
Myxophyceae	191	34	26	251	3	28
Chrysophyceae	16	6	2	24	4	4
Heterokontae	15	5	3	23	1	5
Dinophyceae	11	1	1	13	..	..
Cryptophyceae	...	...	...	...	2	..
Rhodophyceae	2	1	...	3	..	..
Charophyceae	18	3	...	21	..	..
Euglenophyceae	9	2	2	13	6	5
Chlorophyceae	(743)	(210)	(111)	(1,064)	..	..
Volvocales	7	1	4	12	1	1
Tetrasporales	11	6	...	17	1	8
Ulotrichales	56	21	8	85	..	6
Oedogoniales	91	23	2	116	..	..
Chlorococcales	120	20	17	157	3	25
Siphonales	7	5	2	14	..	..
Zygnematales	(451)	(134)	(78)	(663)	..	..
Zygnemataceae	59	24	5	88	..	..
Mesotaeniaceae	21	2	1	24	..	..
Desmidiaceae	371	108	72	551	..	..
Totals	1,005	262	145	1,412	21	82

LIST OF SPECIES

MYXOPHYCEAE

CHROOCOCCALES

APHANOCAPSA DELICATISSIMA W. and G. S. West. — Abundant in Tomahawk Lakes, Presque Isle; Ackley (2).

APHANOCAPSA RIVULARIS (Carm.) Rabenh. — Emmet and Charlevoix; Ackley (2).

APHANOTHECE CLATHRATA W. and G. S. West. — Cheboygan; Welch (43).

APHANOTHECE NIDULANS Richter. — Cheboygan and Emmet; Ackley (2).

Chroococcus giganteus W. West. — Emmet and Charlevoix; Ackley (2).

Gleocapsa gigas W. and G. S. West. — Cheboygan and Emmet; Ackley (2).

Gloeothece lunata W. and G. S. West. — Emmet; Ackley (2).

Gomphosphaeria lacustris Chodat. — Cheboygan and Emmet; Ackley (2).

Marsoniella elegans Lemm. — Emmet, Charlevoix, and Otsego; Taft (29).

Merismopedia punctata Meyen. — Emmet and Otsego; Ackley (2).

*Synechococcus aeruginosus Näg. — Cheboygan.

*Synechococcus aeruginosus Näg. var. maximus Lemm. — Shoepack Lake, Presque Isle.

CHAEMOSIPHONALES

*Xenococcus rivularis (Hansg.) Geitler. — Nichol's Bog, Cheboygan.

The identification is open to some question, although similar material from the same locality has been provisionally assigned to this species by Dr. G. E. Nichols, of Yale University.

HORMOGONALES

Anabaena contorta Bach. — Emmet; Ackley (2).

Anabaena inaequalis (Kütz.) Bornet and Flahault. — Cheboygan and Emmet; Ackley (2).

Anabaena Lemmermanni Richter. — Cheboygan and Otsego; Ackley (2).

Anabaena limnetica G. M. Smith. — Otsego; Raymond (25).

Anabaena torulosa (Carm.) Lagerh. — Cheboygan and Emmet; Ackley (2).

Calothrix parietina (Näg.) Thuret. — Cheboygan, Emmet, and Charlevoix; Ackley (2).

Cylindrospermum minutum Wood. — Emmet; Ackley (2).

Dicothrix Orsiana (Kütz.) Bornet and Flahault. — Presque Isle; Ackley (2).

Hapalosiphon fontinalis (Ag.) Bornet. — Cheboygan and Emmet; Ackley (2).

Lyngbya aerugineo-coerulea (Kütz.) Gom. — Cheboygan; Ackley (2).

Lyngbya major Menegh. — Presque Isle; Ackley (2).

Lyngbya majuscula (Dillwyn) Harvey. — Cheboygan and Charlevoix; Ackley (2).

Microcoleus paludosus (Kütz.) Gom. — Otsego; Velasquez (41).

Nodularia paludosa Wolle. — Presque Isle; Ackley (2).

Nostoc microscopicum Carm. — Emmet and Otsego; Ackley (2).

Nostoc punctiforme (Kütz.) Hariot. — Otsego; Ackley (2).

Phormidium Retzii (Ag.) Gom. — Emmet; Velasquez (41).

Scytonema Hofmanni Ag. — Cheboygan; Ackley (2).

CHRYSOPHYCEAE

*Chrysamoeba radians Klebs. — Cheboygan.

Chrysocapsa planctonica (W. and G. S. West) Pascher. — Emmet and Charlevoix; Taft (29).

*Derepyxis urceolata (Stokes) Lemm. — Presque Isle.

The identification of this species is somewhat doubtful because of the small number of individuals found.

Lagynion ampullaceum (Stokes) Pascher. — Common epiphyte on other algae in Charlevoix; Taft (29).

Mallomonas caudata Iwanoff. — Cheboygan and Emmet; Taft (29).

*Mallomonas tonsurata Teilung. — Rather abundant in several plankton samples taken from Emmet.

*Syncrypta volvox Ehr. — Found in several collections from roadside ditches in Presque Isle.

This species was identified by Dr. Nichols from collections made in 1933 in Vincent Lake, although no record was published.

Uroglena volvox Ehr. — Charlevoix and Otsego; Kofoid (15).

HETEROKONTAE

*Centritractus belenophorus Lemm. — Emmet and Otsego.

There appears to be no previously published record of the occurrence of this species in the United States, although Dr. James B. Lackey, of the United States Public Health Service, Cincinnati, Ohio, has found it to be abundant in Ohio, and the author has collected it in Massachusetts.

Ophiocytium arbusculum (A. Braun) Rabenh. — Charlevoix and Emmet; Ackley (2).

Ophiocytium capitatum Wolle. — Emmet and Presque Isle; Ackley (2).

Ophiocytium majus Näg. — Cheboygan, Emmet, Charlevoix, and Presque Isle; Ackley (2).

Ophiocytium parvulum (Perty) A. Braun. — Present in collections from all counties studied; Ackley (2).

Stipitococcus urceolatus W. and G. S. West. — Otsego and Presque Isle; Taft (29).

CRYPTOPHYCEAE

*Cryptomonas erosa Ehr. — Emmet, Charlevoix, and Presque Isle.

*Cryptomonas ovata Ehr. — Cheboygan, Charlevoix, Emmet, and Presque Isle.

EUGLENOPHYCEAE

*Euglena deses Ehr. — Occasional in plankton; Cheboygan.

Euglena oxyuris Schmarda. — Occasional in vegetable débris in roadside ditches; Cheboygan and Emmet; Dolley (13).

*Lepocinclis ovum (Ehr.) Lemm. — Presque Isle.

Phacus acuminatus Stokes. — Cheboygan and Emmet; Taft (29).

Phacus pleuronectes (O. F. M.) Duj. — Roadside pools; Emmet and Presque Isle; Ackley (2).

Phacus pyrum (Ehr.) Stein. — Cheboygan and Emmet; Taft (29).

*Phacus triqueter (Ehr.) Duj. — Otsego.

*Trachelomonas crebea Kellicott. — Charlevoix and Otsego.

Trachelomonas hispida (Perty) Stein. — Emmet and Presque Isle; Taft (29).

*Trachelomonas urceolata Stokes. — Otsego.

*Trachelomonas volvocina Ehr. — Otsego.

CHLOROPHYCEAE

VOLVOCALES

*Carteria cordiformis (Carter) Diesing. — Cheboygan and Emmet.

Pleodorina californica Shaw. — Emmet; Dolley (13).

TETRASPORALES

*Apiocystis Brauniana Näg. var. linearis Rabenh. — In several collections from Carp River, Emmet, always in association with the species.

Individuals of the species were larger than those usually found elsewhere, the colonies frequently exceeding 800 microns in length.

Asterococcus limneticus G. M. Smith. — Emmet and Presque Isle; Ackley (2).

Asterococcus superbus (Cienk.) Scherffel. — Found frequently in collections from Cheboygan, Emmet, and Charlevoix; reported rare by Ackley (2).

Elakatothrix viridis (Snow) Printz. — Cheboygan and Emmet; Taft (29).

Gloeocystis ampla Kütz. — Cheboygan and Emmet; Taft (29).

Gloeocystis limneticus G. M. Smith. — Emmet; Ackley (2).

Gloeocystis vesiculosa Näg. — Cheboygan and Emmet; Ackley (2).

Sphaerocystis Schroeteri Chodat. — Common in plankton of ponds and lakes in Cheboygan and Emmet; Ackley (2).

Tetraspora gelatinosa (Vauch.) Desvaux. — Cheboygan, Emmet, Charlevoix, Otsego, and Presque Isle; Ackley (2).

ULOTRICHALES

Aphanochaete vermiculoides Wolle. — Cheboygan; Taylor (30).

Chaetosphaeridium globosum (Nordst.) Klebahn. — Cheboygan and Emmet; Ackley (2).

Draparnaldia glomerata (Vauch.) Ag. — Cheboygan; Ackley (2).

Microthamnion Kuetzingianum Näg. — Cheboygan; Taft (29).

Radiofilum conjunctivum Schmidle. — Cheboygan; Taft (29).

Stichococcus bacillaris Näg. — Cheboygan; Ackley (2).

CHLOROCOCCALES

Ankistrodesmus falcatus (Corda) Ralfs var. mirabilis (W. and G. S. West) G. S. West. — Emmet; Taylor (30).

Ankistrodesmus spiralis (Turner) Lemm. — Cheboygan and Emmet; Ackley (2).

Characium ambiguum Herman. — Cheboygan and Presque Isle; Ackley (2).

Characium stipitatum (Bachm.) Wille. — Cheboygan; Ackley (2).
Chlorella vulgaris Beyerinck. — Emmet and Otsego; Ackley (2).
Chlorococcum infusionum (Schrank) Menegh. — Otsego; Ackley (2).
*Coelastrum speciosum (Wolle) Brunnthaler. — Cheboygan.
Crucigenia apiculata (Lemm.) Schmidle. — Emmet and Otsego; Taft (29).
Crucigenia quadrata Morren. — Cheboygan; Ackley (2).
Franceia Droescheri (Lemm.) G. M. Smith. — Presque Isle; Taft (29).
Golenkinia radiata Chodat. — Emmet and Otsego; Taft (29).
*Lagerheimia quadriseta (Lemm.) G. M. Smith. — Emmet.
Nephrocytium limneticum G. M. Smith. — Emmet; Ackley (2).
Pediastrum biradiatum Meyen. — Cheboygan; Ackley (2).
Scenedesmus abundans (Kirchner) Chodat. — Cheboygan, Emmet, Otsego; Ackley (2).
Scenedesmus acuminatus (Lagerh.) Chodat. — Emmet; Ackley (2).
Scenedesmus acutiformis Schroeder. — Emmet; Taft (29).
Scenedesmus arcuatus Lemm. — Emmet; Ackley (2).
Scenedesmus quadricauda (Turp.) Breb. var. maximus W. and G. S. West. — Cheboygan and Emmet; Taft (29).
Scenedesmus quadricauda (Turp.) Breb. var. quadrispina (Chodat) G. M. Smith. — Cheboygan and Emmet; Ackley (2).
Selenastrum minutum (Näg.) Collins. — Cheboygan; Ackley (2).
Sorastrum americanum (Bohlin) Schmidle. — Cheboygan and Charlevoix; Taft (29).
Tetraedron enorme (Ralfs) Hansg. — Cheboygan; Taft (29).
*Tetraedron trigonum (Näg.) Hansg. — Presque Isle.
Tetrastrum heterocanthum (Nordstedt) Chodat. — Emmet; Ahlstrom and Tiffany (4).
Trochiscia obtusa (Reinsch) Hansg. — Cheboygan and Presque Isle; Ackley (2).
Trochiscia reticularis (Reinsch) Hansg. — Cheboygan; Ackley (2).
Westella botryoides (W. West) de Wildeman. — Cheboygan and Emmet; Ackley (2).

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THE ATLANTIC COASTAL PLAIN ELEMENT IN THE FLORA OF KALAMAZOO COUNTY, MICHIGAN

CLARENCE R. HANES

THE Atlantic Coastal Plain species of plants are primarily restricted to the coastal plain from Newfoundland to Florida. Several, however, are found in limited areas in central New York and along the shores of Lake Erie; in the southeastern part of Michigan and in the Grand Rapids region; and especially near the southern end of Lake Michigan in southwestern Michigan and northern Indiana. It is around the southern end of Lake Michigan that they occur in the greatest profusion.

The purpose of this paper is not to explain how or why the plants have come to be in these inland locations, but to present a record of those found in Kalamazoo County and to give their distribution. It is a local treatment intended to make the material accessible to anyone who may in the future wish to devote further study to plants of this type.

It should not be out of place, however, to state that in several papers dealing with the subject evidence has been brought forth to show that the route of migration was along the Hudson-Mohawk Valley, then along the Great Lakes, and finally across Michigan by the Grand River Valley. All this inland penetration occurred, of course, when the lakes and streams had confines much different from the present ones. Recent discoveries of the Atlantic Coastal Plain element in Wisconsin, Minnesota, and Iowa have led some botanists to believe that more of these species came up from the south than had previously been supposed.

In our county these plants are found mainly on the sandy or muddy shores of small lakes and in ponds and marshes or on their borders. A few grow in wet woodlands and several on sandy uplands. *Echinochloa Walteri*, the only one that occurs along or near the Kalamazoo River, grows also on stream borders elsewhere in the county.

These species are restricted in great part to the southwest quarter of Kalamazoo County. In this area are two zones, in each of which there is a congestion of this type of flora. Zone 1 comprises the townships of Schoolcraft and Portage, the western sections of Brady and Pavilion townships, and White Lake, near the southern boundary of Kalamazoo Township. Austin Lake is the nucleus of this zone. Zone 2 is composed of Prairie Ronde and Texas townships and a part of Oshtemo Township, with Eagle Lake as its nucleus. Now and then one or more plants of this class have been collected in scattered locations outside these two zones. Stony Lake, in Ross Township, which is the northeastern township of the county, is an exception, since at least nine species grow in the neighborhood of this lake.

The list of plants of this type given by Peattie in *Rhodora*[1] has been used as a guide in selecting those of Kalamazoo County that belong to the group. Several others have been added, since their distribution appears to place them without question in this class. There is some doubt, however, about the following five species, namely: *Eleocharis pauciflora* var. *Fernaldii*, *Rhexia virginica*, *Monardo punctata* var. *villicaulis*, *Melampyrum lineare* var. *latifolium*, and *Utricularia cornuta*. The fact that these five plants which occur on the coast are found in Indiana only in the northern or northwestern part and in Kalamazoo County only in the two zones mentioned has led me to include them in this group.

Specimens of all the species given in the following list have been collected during the past eight years by Mrs. Florence N. Hanes and the writer and are deposited in our herbarium. Many duplicates have been distributed in various herbaria in the United States. The order of locations in the list shows the relative abundance of the species collected.

List of Species

Woodwardia virginica (L.) Sm. — Usually on the border of blueberry swamps in Schoolcraft, Portage, and Prairie Ronde townships. One station outside the restricted area is in Section 8, Climax Township.

Najas gracillima (A. Br.) Morong. — Infrequent in Eagle and Pretty lakes. Abundant in 1938 in Bonnie Castle Lake.

[1] Peattie, D. C., "The Atlantic Coastal Plain Element in the Flora of the Great Lakes," *Rhodora*, 24: 86–88. 1922.

Stipa avenacea L. — On wooded knolls near Sugarloaf, Dustin, and Goose lakes, Section 17, Oshtemo Township. Outside the restricted area near Spring Brook in Richland Township.

Panicum meridionale Ashe. — In marshes near West and Austin lakes; Eagle Lake; White Lake.

Panicum albemarlense Ashe. — Shores of Austin and West lakes; Stony Lake.

Echinochloa Walteri (Pursh) Heller. — Along Flowerfield Creek, Prairie Ronde Township, and the outlet of Barton Lake; also along the Kalamazoo River both east and north of Kalamazoo.

Hemicarpha micrantha (Vahl.) Britt. — On the sandy shores of Eagle, Pretty, Crooked, and Pine Island lakes, all in Texas Township; Bonnie Castle Lake in Oshtemo Township; West and Austin lakes in Portage Township; and Pickerel Lake in Pavilion Township.

Fuirena pumila Torr. — Shores of Eagle, Crooked, Pine Island, and Weeds lakes in Texas Township; East Lake in Pavilion Township; and Stony Lake in Ross Township. The species extends across the county, making jumps of several miles between stations.

Scirpus debilis Pursh var. Williamsii Fern. — Shores of Eagle, Pine Island, and Bonnie Castle lakes. In 1937 this species was found at Pretty Lake in several inches of water.

Scirpus Smithii Gray. — Shores of Weeds and Pickerel lakes and on the east side of Austin Lake.

Eleocharis equisetoides (Ell.) Torr. — In shallow water at White Lake. In the shallow water of Mud Lake, Portage Township, it covers several acres.

Eleocharis quadrangulata (Michx.) R. & S. var. crassior Fern. — Near the southeast shore of Pickerel Lake. Here it grows in one foot or more of water, but after several dry seasons it thrives in the mud.

Eleocharis Robbinsii Oakes. — In shallow water or in mud in marshes west and southwest of West Lake.

Eleocharis melanocarpa Torr. — On the east and the southeast shores of Austin Lake; Bonnie Castle and Pretty lakes. Frequent in several stations around Eagle Lake. It was first collected at Austin Lake in 1934 and was sent to H. R. Svenson for confirmation in 1937. This sedge has recently been collected by C. W. Bazuin in several localities near Grand Rapids.

Peattie uses *E. melanocarpa* as an example of the species which make the jump from the coast to the southern end of Lake Michigan in Indiana without being found at any intermediate points.[2] These Kalamazoo County and Grand Rapids reports supply at least two intermediate stations.

Eleocharis rostellata Torr. — In wet marshes around Sugarloaf, Bonnie Castle, and Pawpaw lakes it is abundant. Outside the restricted zones it is found near Lyon and Three Lakes and at Cold Springs, Alamo Township.

Eleocharis pauciflora (Lightf.) Link. var. Fernaldii Svenson. — In marly soil near the shore of Pawpaw Lake.

Fimbristylis autumnalis (L.) R. & S. var. mucronulata (Michx.) Fern. — Shores of Eagle, Harrison, White, Weeds, West, Austin, Pickerel, Dustin, and Stony lakes.

Psilocarya scirpoides Torr. — Shores of Eagle and Stony lakes; marsh near West Lake; marsh bordering Mud Lake, Texas Township.

Rhynchospora macrostachya Torr. — In marshes west and southwest of West Lake; "Island" marsh near the village of Schoolcraft; Weeds, Mud, Eagle, and Crooked lakes, all in Texas Township. On the eastern shore of Crooked Lake it is abundant in shallow water over an area of several acres.

Rhynchospora fusca (L.) Ait. f. — The only station known to us is in a swamp west of West Lake, where it grows abundantly in sphagnum.

Carex Howei Mack. — In moist woods, often in water. Two stations near Goose Lake, Schoolcraft Township; Section 32, Prairie Ronde Township.

Carex Richii (Fern.) Mack. — Grows in large clumps in a swamp on the north boundary of Section 12 and on the south boundary of Section 1, Schoolcraft Township. Also one mile north of this station on the north boundary of Section 1.

Carex Longii Mack. — In open or thinly wooded swamps. Two stations each in Portage, Schoolcraft, and Pavilion townships. We have collected it in Flowerfield Township, St. Joseph County, and F. W. Rapp has found it in two localities in Brady Township.

Carex albolutescens Schwein. — In thin low woodlands. Section

[2] Peattie, *op. cit.*, pp. 59–60.

33, Portage Township; Section 1, Schoolcraft Township. F. W. Rapp has found it in Section 31, Brady Township, and we have a collection from Portage Lake, St. Joseph County.

Carex alata Torr. — In open swamps. Three stations in Portage Township; Section 32, Brady Township; and Section 22, Schoolcraft Township.

Carex Emmonsii Dewey. — In poplar or blueberry swamps mainly in the open. It is abundant northeast of Goose Lake and near the Jenkinson School in Brady Township. It occurs also in Texas, Prairie Ronde, and Pavilion townships.

Peltandra virginica (L.) Kunth. — Lakes or creeks in Portage, Schoolcraft, and Brady townships.

Xyris caroliniana Walt. — In swamps and on the boggy borders of lakes. Near West, Austin, and Thrall lakes; Le Fevre Bog in Section 8, Climax Township. We have collected this species at Pleasant Lake, Barry County.

Xyris torta Sm. — In damp sandy soil on or near the shores of Eagle, Pretty, and Pine Island lakes.

Juncus Greenei Oakes & Tuckerm. — On sandy lake shores. East shore of Austin Lake and south shore of Eagle Lake.

Juncus balticus Willd. var. littoralis Engelm. f. dissitiflorus Engelm. — On sandy lake shores and borders of swamps. Shores of Eagle, Pretty, and Austin lakes. Border of swamp east of Sugarloaf Lake.

Juncus pelocarpus E. Mey. — On lake borders and in swamps. Borders of Eagle, Austin, Pickerel, Bonnie Castle, and Stony lakes; swamp east of Gourdneck Lake.

Juncus scirpoides Lam. — Abundant on the sand dunes on the east shore of Austin Lake.

Juncus biflorus Ell. — Near the bank of Vicksburg Creek, south of Vicksburg; in low thinly wooded meadow in Section 18, Texas Township. We have also collected this species two miles north of Sturgis, in St. Joseph County.

Quercus prinoides Willd. — Frequent in the sandy parts of Portage, Texas, and Oshtemo townships, along roadsides, in thickets, and sometimes in fields.

Drosera intermedia Hayne. — Near West and Pickerel lakes; on the south side of Pine Island Lake; in Le Fevre Bog, Section 8, Climax Township.

Lupinus perennis L. — Sandy soil of Portage, Pavilion, Texas, Kalamazoo, and Oshtemo townships.

Linum striatum Walt. — On the moist north and south shores of Bonnie Castle Lake.

Polygala cruciata L. — In semimoist soil southwest of West Lake and west of Pine Island Lake in Section 18, Texas Township. Very rare at the latter station.

Lechea minor L. — In sandy soil east of Sugarloaf Lake and near the south shore of Eagle Lake.

Lechea Leggettii Britt. & Holl. var. moniliformis (Bickn.) Hodgdon. — Sand dunes on the east shore of Austin Lake, where it is plentiful.

Rotala ramosior (L.) Koehne var. typica Fern. & Grisc. — Makes an abundant growth on marshes which have recently been burnt over. Marsh southwest of West Lake; swamp east of Gourdneck Lake; ditch south of Hogset Lake; Thrall and Eagle lakes.

Rhexia virginica L. — Sandy borders of Eagle and Pine Island lakes. Very scarce.

Hydrocotyle umbellata L. — On creek and lake borders. At Eagle, Austin, East, White, Sugarloaf, Woods, and Crooked lakes; south of Butterfield Lake in Ross Township; near Flowerfield Creek in Section 20, Prairie Ronde Township.

Stachys hyssopifolia Michx. — Sandy soil near the shores of Eagle, White, West, Sugarloaf, Austin, Stony, and Gourdneck lakes; borders of several marshes in Prairie Ronde and Texas townships. Sandy fields in Section 17, Oshtemo Township, and Section 32, Portage Township.

Monarda punctata L. var. villicaulis Pennell. — Texas, Portage, and Oshtemo townships. On the east side of the county it is found west of Stony Lake.

Linaria canadensis (L.) Dumont. — Frequent in the west part of the county near Sugarloaf and Hampton lakes, in Section 7, Oshtemo Township, and in Section 23, Alamo Township. Also west of Spring Brook in Cooper Township.

Gerardia purpurea L. — On sandy lake shores. Austin and Duck lakes.

Melampyrum lineare Lam. var. latifolium (Muhl.) Beauv. — Sandy soil east of Sugarloaf Lake in Section 4, Schoolcraft

Township, and in Section 35, Prairie Ronde Township. Near Austin and Goose lakes.

Utricularia gibba L. — Muddy borders of lakes and creeks. Of the thirteen locations known to us in the county all are in the restricted area with the exception of two, which are at Stony Lake, Ross Township, and in Le Fevre Bog in Section 8, Climax Township.

Utricularia purpurea Walt. — The only station known to us is at White Lake, Kalamazoo Township, where it grows in 12 to 18 inches of water.

Utricularia resupinata B. D. Greene. — In shallow water on the borders of Austin, Pickerel, White, Eagle, and Pretty lakes. Change of water level affects its abundance.

Utricularia cornuta Michx. — On the marshy border of Mud Lake, north of Sugarloaf Lake; near the east shore of Pawpaw Lake. Scarce at both locations. We have collected this species at Pleasant Lake, Barry County.

Bidens discoidea (T. & G.) Britt. — In a swampy thicket one mile northeast of Vicksburg in the northwest quarter of Section 8, Brady Township.

Kalamazoo County has sixteen townships, with a total land and water area of 575 square miles. The frequency of the 54 Atlantic Coastal Plain species listed is as follows in the various townships: Portage, 38; Texas, 32; Schoolcraft, 20; Oshtemo, 15; Pavilion, 13; Prairie Ronde, 10; Brady, 9; Ross, 9; Kalamazoo, 9, of which eight are near White Lake; Climax, 4; Alamo, 3; Cooper, 2; Richland, 2; Comstock, 1; Charleston, 0; and Wakeshma, 0.

Schoolcraft, Michigan

LICHENS IN AND NEAR THE OLYMPIC NATIONAL PARK, WASHINGTON *

JOYCE HEDRICK

THE specimens upon which this report is based were collected by A. H. Smith, of the University of Michigan, in September and October of 1935 and during April, May, and June of 1939. They number over 600. The present paper consists of a list of 146 species and subspecies based on 465 specimens, which have been deposited in the Herbarium of the University of Michigan.

The collecting was done in and near the Olympic National Park, Washington. The main region covered extends from Port Angeles to Lake Crescent, along the southern shore of Lake Crescent, Storm King Mountain, then south to Deer Lake and east to Boulder Peak and Olympic Hot Springs, along the Elwha River and up the trail along Hurricane Ridge to Steeple Peak and Obstruction Point. Other specimens were found farther west in the state, along the Pysht River, at Cape Flattery, around Lake Ozette, along the Hoh River, and south to the Clearwater River.

Incidental collections were made at elevations ranging from sea level to 2,500 feet. Special care was taken to collect on the rock exposures in the higher elevations. Intensive collecting was done on Storm King Mountain, up to 4,500 feet, and on Boulder Peak at an elevation of 5,000 to 7,000 feet. Elevations less than 2,500 feet are not given in the list.

Lists and descriptions of lichens from Washington have been published by Tuckerman (1866, 1883, 1884), Müller (1889), Merrill (1908, 1909, 1910, 1911, 1913, 1914), Fink (1919), and Magnusson (1932). More extensive work has been done by Herre (1917) in a paper based on the lichens of Whatcom County and by Howard (1937) in a report of her collections throughout the state. Howard lists 283 species and subspecies and observes that no really exhaustive collecting was done in any one region.

* Papers from the Herbarium of the University of Michigan.

So far as I have been able to ascertain, the 18 species and 4 subspecies marked with an asterisk (*) in this account have not been previously reported from the state of Washington.

List of Species

PYRENULACEAE

Pyrenula laevigata (Pers.) Ach. — On alder, Cape Flattery, 1890a, 1895.

Pyrenula nitida (Weig.) Ach. — On alder, Cape Flattery, 13151.

CALICICACEAE

*Calicium Curtisii Tuck. — On conifer trees and pitch of fir, Deer Lake Trail, 14314, 14316.

*Calicium trachelinum Ach. — On decorticate trees and logs, Hurricane Ridge, 2364, 2371; Lake Angeles, 14647.

Coniocybe furfuracea (L.) Ach. — On rocks at base of tree, Lake Crescent, 2281, 2284, 11136.

CYPHELIACEAE

Cyphelium inquinans (J. E. Smith) Trevis. — On old stumps, Storm King Mountain, 2275.

*Cyphelium ventriculosum (Müll. Arg.) Zahlbr. — On old stump, Lake Crescent, 2253.

SPHAEROPHORACEAE

Sphaerophorus globosus (Huds.) Vainio. — On old logs and fallen trees, Olympic Hot Springs, 1965, 1996, 2003, 2121; Lake Crescent, 1833, 1956, 2263, 2282; Elwha River, 2304; Boulder Lake Trail at 4,500 ft., 13816.

ARTHONIACEAE

Arthonia excedens Nyl. — On alder, Cape Flattery, 1906.

Arthonia radiata (Pers.) Ach. — On bark, Pyscht River, 1919a.

GRAPHIDACEAE

Opegrapha varia Pers. — On twigs of tree, Cape Flattery, 13781, 13786.

Graphis scripta (L.) Ach. — On alder, Cape Flattery, 1906a; Pyscht River, 1914; Olympic Hot Springs, 2149; Hoh River, 13367, 13369, 13373.

Graphis scripta var. serpentina (Ach.) Meyer. — On alder, Pyscht River, 1916; Hoh River, 13374.

THELOTREMACEAE

Thelotrema lepadinum Ach. — On alder, Olympic Hot Springs, 1993.

DIPLOSCHISTACEAE

Diploschistes scruposus (Schreb.) Norm. — On rocks, Storm King Mountain at 3,500 ft., 2231, 2255.

COLLEMACEAE

Leptogium palmatum (Huds.) Mont. — On moss, Hoh River, 13361.

PANNARIACEAE

Parmeliella lepidiota (Sommerf.) Vainio. — On bark, Olympic Hot Springs, 1979; Deer Lake Trail, 13413.

*Parmeliella corallinoides (Hoffm.) Zahlbr. — At base of tree, Lake Crescent, 13836.

Pannaria granatina (Sommerf.) T. Fries. — On rock, talus slope, Olympic Hot Springs, 2102; Storm King Mountain at 4,000 ft., 2212.

Pannaria pezizoides (Weberi) Trevis. — On soil, Boulder Peak at 6,000 ft., 2741; on moss, Deer Lake Trail at 3,500 ft., 14329.

*Pannaria leucosticta Tuck. — On rocks, Olympic Hot Springs, 1991, 1997, 2154.

Psoroma hypnorum (Vahl.) S. F. Gray. — Over moss and débris, Olympic Hot Springs at 3,500–4,000 ft., 1968, 2120; Steeple Peak at 5,000 ft., 2323.

STICTACEAE

Lobaria oregana (Tuck.) Müll. Arg. — Over rocks, Deer Lake Trail, 13342.

Lobaria pulmonaria (L.) Hoffm. — On trees, Olympic Hot Springs, 1995, 20001, 2004; Hoh River, 13235.

Sticta anthraspis Ach. — On alder, Cape Flattery, 13127.

PELTIGERACEAE

Solorina crocea (L.) Ach. — On soil and moss, Boulder Peak at 6,000 ft., 2918.

Nephroma resupinatum (L.) Ach. — On alder, Olympic Hot Springs, 2109; Cape Flattery, 13125, 13126.

Peltigera aphthosa (L.) Willd. — On old logs, débris, soil, and humus, Lake Crescent, 1830, 2244, 2245, 2247; Olympic Hot Springs, 1980; Boulder Peak at 6,000 ft., 2904; Deer Lake Trail, 13346.

Peltigera venosa (L.) Baumg. — On soil, Lake Crescent, 2273.

Peltigera polydactyla (Neck.) Hoffm. — Over old tree and log, Olympic Hot Springs, 2122; Clearwater River, 13272; Kalaloch, 13324.

Peltigera scutata (Dicks.) Duby. — On alder, Cape Flattery, 1894.

Peltigera canina (L.) Willd. — On débris, soil, old logs, and moss, Olympic Hot Springs, 1984; Steeple Peak at 5,000 ft., 2317, 2318, 2324; Kalaloch, 12071, 12075; Hoh River, 13357.

Peltigera canina var. membranacea (Ach.) Duby. — On old logs, over soil and moss, Clearwater River, 13278; Kalaloch, 13326, 13327, 13329; Lake Ozette, 13744.

LECIDEACEAE

*Lecidea vernalis (L.) Ach. — On twigs, rotten wood, and over moss, Olympic Hot Springs, 1987, 2127, 2129, 2156; Steeple Peak at 5,000 ft., 2314; Boulder Peak at 6,000 ft., 2908.

Lecidea cinnabarina Fée. — On bark, fallen trees, and old stump, Olympic Hot Springs at 4,000 ft., 2005; Hurricane Ridge at 5,500 ft., 2360a, 2386, 2387; Cape Flattery, 13792; Boulder Lake Trail, 13819a.

Lecidea carnulenta (Tuck.) Fink. — On bark, Olympic Hot Springs, 1972, 1976, 1992; on old wood, Hurricane Ridge at 5,500 ft., 2380; Crystal Ridge, 14991.

Lecidea granulosa (Hoffm.) Ach. — On old and burned wood, over soil and débris, Storm King Mountain at 3,500 ft., 2214, 2233; Steeple Peak at 5,000 ft., 2322, 2328, 2329; Hurricane Ridge at 5,500 ft., 2367, 2372, 2379, 2389; Boulder Peak at 5,500–6,000 ft., 2916, 2921.

*Lecidea melancheima Tuck. — On old wood, Hurricane Ridge at 5,500 ft., 2383, 2390, 14863.

Lecidea fuscescens Sommerf. — On trees, Hurricane Ridge at 5,500 ft., 2360, 2417.

Lecidea enteroleuca Ach. — On rocks, Steeple Peak at 5,300 ft., 2342; Hurricane Ridge at 6,000 ft., 2410, 2418a.

Lecidea platycarpa Ach. — On rocks, talus slope, Olympic Hot Springs at 3,500 ft., 1966, 1989, 1992, 2087, 2092, 2159; Hurricane Ridge at 5,500 ft., 2384a, 2392; Boulder Peak at 5,500–6,000 ft., 2730, 2739, 2861, 2888, 2891, 2896, 2902.

Lecidea lapicida Ach. — On rocks, talus slope, Olympic Hot Springs, 2134; Storm King Mountain at 3,500 ft., 2241, 2243a; Steeple Peak at 5,300 ft., 2341; Boulder Peak at 5,500–6,000 ft., 2721, 2722, 2731, 2736, 2856a, 2866.

Lecidea albocaerulescens var. flavocaerulescens Schaer. — On rocks and talus slope and along stream, Olympic Hot Springs, 2112, 2124; Storm King Mountain at 4,300 ft., 2267; Boulder Peak at 5,500 ft., 2860, 2863b, 2871.

Lecidea atrobrunnea (Ram.) Schaer. — On rocks, Storm King Mountain at 3,800 ft., 2249, 2250.

Lecidea fuscoatra (L.) Ach. — On rocks, Storm King Mountain at 3,500–4,000 ft., 2221, 2232, 2237, 2252, 2257, 2265, 2279; Hurricane Ridge at 6,000 ft., 2399a; Boulder Peak at 5,500 ft., 2862, 2863a, 2875, 2882, 2894, 2904.

Psora ostreata Hoffm. — On old wood, Olympic Hot Springs, 1994.

*Nesolechia vitellinaria (Nyl.) Rehm. — On the thallus of *Candelariella vitellina*, Boulder Peak at 6,000 ft., 2726.

Mycoblastus sanguinarius (L.) Norm. — On bark, Lake Crescent, 1951, 2280; Olympic Hot Springs, 1958; Elwha River, 2308, 2310; Boulder Peak at 5,500 ft., 2905; Kalaloch, 13011; Boulder Lake Trail, 13819a; Crystal Ridge, 14989, 14990.

Mycoblastus alpinus (E. Fries) Kernst. — On bark and old stumps, Olympic Hot Springs, 1969, 1971, 1983, 1986; Lake Crescent, 2240; Hurricane Ridge at 5,500 ft., 2365, 2422, 2433; Deer Lake Trail, 14313.

Catillaria tricolor (With.) T. Fries. — On bark, Elwha River, 2306.

*Catillaria franciscana (Tuck.) Herre. — On rocks, Storm King Mountain at 3,800–4,000 ft., 2270, 2277.

*Bacidia flavovirescens (Dicks.) Anzi. — On débris, Storm King Mountain at 4,000 ft., 2213.

Lopadium pezizoideum (Ach.) Koerb. — On alder, Olympic Hot Springs at 3,500 ft., 1967, 1978, 2130, 2137.

*Rhizocarpon oederi (Web.) Koerb. — On rocks, talus slope, Olympic Hot Springs, 2086.

Rhizocarpon petraeum (Wulf.) Mass. — On rocks, Storm King Mountain at 3,500 ft., 2216, 2254.

Rhizocarpon penichrum (Tuck.) Merrill. — On bark, Lake Crescent, 2253a, 13983; on old stump, Storm King Mountain at 3,000 ft., 2229, 2260, 2272.

Rhizocarpon lecanorinum (Koerb.) Anders. — On rocks, talus slope, Olympic Hot Springs, 2098.

Rhizocarpon geographicum (L.) Lam. & DC. — On rocks, talus slope, Olympic Hot Springs, 2081; Steeple Peak at 5,300 ft., 2334; Hurricane Ridge, 2399, 2428, 2432, 2434; Boulder Peak at 5,500 ft., 2853, 2856, 2859, 2868, 2877, 2879.

Rhizocarpon oidaleum (Tuck.) Fink. — On old tree, Lake Crescent, 2276.

CLADONIACEAE

Pilophorus cereolus (Ach.) T. Fries. — On rocks, Lake Crescent, 1837; Olympic Hot Springs at 3,500–4,000 ft., 1976; Deer Lake Trail, 13340.

Cladonia rangiferina (L.) Web. — Among and over mossy rocks, talus slope, Olympic Hot Springs, 2085, 2111, 2118, 2131, 2151.

Cladonia sylvatica (L.) Hoffm. — Over rocks, base of talus slope, Olympic Hot Springs, 2079a.

Cladonia macilenta Hoffm. — On old log and stump, Cape Flattery, 1892, 1896; Lake Crescent, 1952, 1954.

Cladonia bellidiflora (Ach.) Schaer. — On soil and old logs, talus slope, Olympic Hot Springs, 1981, 2132; Boulder Peak at 5,500 ft., 2911, 2960; Kalaloch, 13161; Hoh River, 13637.

Cladonia bellidiflora var. coccocephala (Ach.) Vainio. — Over and among rocks, along stream, Olympic Hot Springs, 2116; Hurricane Ridge at 5,500 ft., 2381.

Cladonia uncialis (L.) Hoffm. — On débris, Storm King Mountain at 4,000 ft., 2215.

Cladonia furcata (Huds.) Schrad. — On soil and débris, Lake Crescent, 1832; Storm King Mountain at 3,800 ft., 11130.

Cladonia furcata var. racemosa (Hoffm.) Floerke. — On soil, Lake Crescent, 1831, 11131, 11132; Storm King Mountain at 3,000 ft., 2271; Hoh River, 13644.

Cladonia furcata var. pinnata (Floerke) Vainio. — On soil, Storm King Mountain at 3,000 ft., 2223; Hoh River, 13640; near trail, Lake Crescent, 13849.

*Cladonia furcata var. scabriuscula (Del.) Vainio. — On exposed soil, Lake Crescent, 1834.

Cladonia furcata var. palamaea (Ach.) Nyl. — On débris and over rocks, Storm King Mountain at 3,000 ft., 2227; at lake edge, Lake Crescent, 13837.

Cladonia squamosa (Scop.) Hoffm. — Among rocks, talus slope, Olympic Hot Springs, 2106.

Cladonia squamosa var. denticollis (Hoffm.) Floerke. — On soil, Boulder Peak at 5,500 ft., 2922, 2924.

Cladonia subsquamosa (Nyl.) Vainio. — On old logs and débris, Lake Crescent, 1953, 2256; Crescent Beach, 2976, 2981; Kalaloch, 13164; Hoh River above Jackson Guard Station, 13382; Hoh River, 13636.

Cladonia cenotea (Ach.) Schaer. — On old log, Crescent Beach, 2974.

Cladonia cariosa (Ach.) Spreng. — On soil, Steeple Peak at 5,000 ft., 2321.

Cladonia gracilis (L.) Willd. — On soil, Boulder Peak at 6,000 ft., 2907.

Cladonia gracilis var. ecmocyna (Ach.) Scriba. — On soil, Steeple Peak at Obstruction Point Road, 2315; Hurricane Ridge at 5,500 ft., 2374; Boulder Peak at 6,000 ft., 2906; Crystal Ridge, 14985.

Cladonia gracilis f. anthocephala Floerke. — On soil, Steeple Peak at Obstruction Point Road, 2316; Hurricane Ridge at 5,500 ft., 2359, 2373, 2375, 2378; Boulder Peak at 5,500 ft., 2913.

Cladonia gracilis var. dilatata (Hoffm.) Vainio. — On soil, Hurricane Ridge at 5,500 ft., 2361, 2362.

Cladonia gracilis var. chordalis (Floerke) Schaer. — On soil and among rocks, base of talus slope, Olympic Hot Springs, 2079, 2080; Bogachiel Ridge at 5,500 ft., 2719; Boulder Peak at 6,000 ft., 2915.

*Cladonia gracilis var. aspera Floerke. — On soil, Boulder Peak at 6,000 ft., 2923.

*Cladonia gracilis var. elongata (Jacq.) E. Fries. — Over mossy rocks, talus slope, Olympic Hot Springs, 2117.

Cladonia gracilescens (Floerke) Vainio. — On cedar stump, Olympic Hot Springs, 1998.

Cladonia pyxidata (L.) Hoffm. — On soil, Hurricane Ridge at 5,500 ft., 2370; Storm King Mountain, 14275.

Cladonia pyxidata var. chlorophaea (Ach.) Flot. — On soil and débris, Olympic Hot Springs, 2139; Lake Crescent, 11133.

Cladonia verticillata var. cervicornis (Ach.) Flot. — On soil, talus slope, Olympic Hot Springs, 2142.

Cladonia fimbriata var. simplex (Weiss.) Flot. — On thin soil over rocks, Lake Crescent, 1835.

Cladonia fimbriata var. subulata (L.) Vainio. — On soil over old logs, Hurricane Ridge at 5,500 ft., 2420.

Cladonia fimbriata var. coniocraea (Floerke) Vainio. — On old log, Hurricane Ridge at 5,500 ft., 11134.

Cladonia fimbriata var. ochrochlora (Floerke) Vainio. — On old log and débris, Cape Flattery, 1888; talus slope, Olympic Hot Springs, 2135, 2138.

*Cladonia cyanipes (Sommerf.) Vainio. — On soil over wood, Hurricane Ridge at 5,500 ft., 2368.

Cladonia carneola (Ach.) Spreng. — On débris, Storm King Mountain at 3,000 ft., 2228.

Cladonia carneola var. prolifera Flot. — On rotten wood, Hurricane Ridge at 5,500 ft., 2363.

Stereocaulon paschale var. conglomeratum E. Fries. — On soil over rocks, Storm King Mountain at 3,500 ft., 2238.

Stereocaulon tomentosum E. Fries. — Over rocks along stream, Olympic Hot Springs, 2105, 2108, 2113, 2133; on débris, Storm King Mountain at 3,500 ft., 2262; on dry sandy soil, Hoh River bank above Jackson Guard Station, 13412.

Stereocaulon tomentosum var. simplex Riddle. — Over rocks, Storm King Mountain, 14273.

UMBILICARIACEAE

Umbilicaria hyporborea Ach. — On rocks, Hurricane Ridge at 6,000 ft., 2395, 2401; Boulder Peak at 6,000 ft., 2912.

Umbilicaria proboscidea (L.) Schrad. — On rocks, Hurricane Ridge at 6,000 ft., 2397a; Boulder Peak at 6,000 ft., 2867, 2887.

ACAROSPORACEAE

*Biatorella resinae (E. Fries) T. Fries. — On wounds of conifer tree, Deer Lake Trail, 14315, 14319; on débris over rocks, Crystal Ridge, 14993.

PERTUSARIACEAE

Pertusaria multipuncta (Turn.) Nyl. — On alder, Olympic Hot Springs, 2125.

*Pertusaria velata (Turn.) Nyl. — On fallen hemlock, Lake Ozette, 13433.

LECANORACEAE

Lecanora gibbosa (Ach.) Nyl. — On rocks, Hurricane Ridge at 5,500 ft., 2427; Boulder Peak at 6,000 ft., 2876.

Lecanora laevata (Ach.) Nyl. — On rocks along stream, Olympic Hot Springs, 2147.

Lecanora cinerea (L.) Röhling. — On rocks, Storm King Mountain at 3,000–3,800 ft., 2218, 2243, 2282; Steeple Peak at 5,300 ft., 2335, 2337, 2338, 2340; Hurricane Ridge at 6,000 ft., 2410a, 2418, 2419, 2434a; Boulder Peak at 5,500 ft., 2874.

*Lecanora glaucomela Tuck. — On alder, Olympic Hot Springs, 2146; Deer Lake, 13414, 14328.

Lecanora alpina Sommerf. — On rocks, Storm King Mountain at 3,500 ft., 2230.

Lecanora subfusca (L.) Ach. — On alder, Pyscht River, 1913, 1920; Olympic Hot Springs, 2158.

Lecanora subfusca var. argentata Ach. — On alder, Hoh River, 13360, 13362a, 13370.

Lecanora pacifica Tuck. — On trees, Lake Crescent, 1949, 13833, 13854, 14385; Cape Flattery, 13139.

Lecanora polytropa (Ehrh.) Rabenh. — On rocks, talus slope, Olympic Hot Springs, 2090; Storm King Mountain at 4,000 ft., 2242; Steeple Peak at 5,000 ft., 2312, 2313; Hurricane Ridge at 6,000 ft., 2393, 2404, 2406, 2414; Boulder Peak at 5,500 ft., 2738, 2886.

Lecanora polytropa var. alpigena (Ach.) Rabenh. — On rocks, Steeple Peak at 5,000 ft., 2327; Hurricane Ridge at 6,000 ft., 2408; Boulder Peak at 5,500 ft., 2890.

Lecanora polytropa var. illusoria (Ach.) Leight. — On rocks, Hurricane Ridge at 5,500 ft., 2369, 2384.

Lecanora rupicola (L.) Zahlbr. — On rocks, Hurricane Ridge at 6,000 ft., 2396, 2405, 2408, 2409, 2415; Boulder Peak at 6,000 ft., 2733.

Lecanora gelida (L.) Ach. — On rocks, Lake Crescent, 1836; Storm King Mountain at 3,500–3,800 ft., 2251, 14994a; Boulder Peak at 5,500 ft., 2885.

Ochrolechia tartarea (L.) Mass. — On old log and trees, Lake Crescent, 1955, 2246; Elwha River, 2307, 2309; Kalaloch, 13011a; Boulder Lake Trail at 4,500–6,600 ft., 13805, 13819; Crystal Ridge, 14988.

Ochrolechia pallescens (L.) Mass. — On trees, Pyscht River, 1909, 1911; Olympic Hot Springs, 2136, 2140, 2157; Cape Flattery, 13146; Hoh River, 13362, 13365, 13367.

Ochrolechia pallescens var. rosella Tuck. — On trees, Olympic Hot Springs, at 2,500–4,000 ft., 1964, 1973, 1985, 2002.

Ochrolechia upsaliensis (L.) Mass. — On débris, Boulder Peak at 6,000 ft., 2910; Storm King Mountain at 4,000 ft., 11137.

Icmadophila ericetorum (L.) Zahlbr. — On old wood, Lake Crescent, 1838, 2069, 13844; Olympic Hot Springs, 1962; Oil City, 13103.

Candelariella vitellina (Ehrh.) Müll. Arg. — On rocks, Storm King Mountain at 3,500–3,800 ft., 2219, 2236, 14994.

parmeliaceae

Parmelia physodes var. enteromorpha Tuck. — On trees, Cape Flattery, 1904; Olympic Hot Springs at 2,500 3,000 ft., 1963; Boulder Lake Trail at 6,500 ft., 13804.

Parmelia physodes var. vittata Ach. — On trees, Olympic Hot Springs, 13802.

Parmelia pertusa (Schrank.) Schaer. — On trees, Pyscht River, 1908, 1912; Olympic Hot Springs, 2107; Hurricane Ridge at 5,500 ft., 2416.

Parmelia perlata (L.) Ach. — On trees, Cape Flattery, 1891, 1893; Boulder Peak at 5,500 ft., 2919.

Parmelia saxatilis (L.) Ach. — On rocks, Boulder Peak at 5,500 ft., 2872.

Parmelia sulcata Tayl. — On rocks, Olympic Hot Springs, 2156.

*Parmelia colpodes (Ach.) Nyl. — On trees, Olympic Hot Springs, 1974, 1975; Hurricane Ridge at 5,500 ft., 2376, 2385, 2391; Crystal Ridge, 14984.

Cetraria glauca (L.) Ach. — On trees, Boulder Lake Trail at 6,500 ft., 13803, 13804.

Cetraria platyphylla Tuck. — On trees, Crystal Ridge, 14981.

Cetraria islandica (L.) Ach. — On trees, Hurricane Ridge at 5,500 ft., 2358; Crystal Ridge, 14980.

*Cetraria tristis (Web.) E. Fries. — On rocks, Hurricane Ridge at 6,000 ft., 2394, 2397, 2400, 2402.

USNEACEAE

*Alectoria divergens (Ach.) Nyl. — On rocks, Hurricane Ridge at 6,000 ft., 2401a.

Alectoria implexa (Hoffm.) Röhling. — On trees, Hurricane Ridge at 5,500 ft., 2377, 2421.

Alectoria sarmentosa Ach. — On trees, Olympic Hot Springs at 2,500–4,000 ft., 1970; Elwha River, 2305; Hurricane Ridge at 5,500 ft., 2377a, 2421a; Kalaloch, 13152; Crystal Ridge, 14982, 14983.

Ramalina farinacea (L.) Ach. — On trees, Cape Flattery, 1889a, 1902, 13130, 13132, 13148.

Usnea florida (L.) Web. — On trees, Cape Flattery, 1897a, 1900, 1902a, 13124, 13150.

Usnea plicata (L.) Web. — On trees, Cape Flattery, 1897.

Usnea barbata (L.) Wigg. — On trees, Cape Flattery, 1889, 1897b, 1899.

Thamnolia vermicularis (Swartz) Schaer. — On débris and soil, Storm King Mountain at 3,800 ft., 2211; Boulder Peak at 6,000 ft., 2914, 2920.

CALOPLACACEAE

Caloplaca cerina (Ehrh.) T. Fries. — On twigs, Lake Crescent, 14360.

Caloplaca ferruginea (Huds.) T. Fries. — On trees, Cape Flattery, 1890, 1901, 13142; Lake Crescent, 13832.

TELOSCHISTACEAE

Teloschistes candelarius (L.) Fink. — On alder, Cape Flattery, 13149.

BUELLIACEAE

Buellia parasema (Ach.) Denot. — On alder, Pyscht River, 1917, 1918, 1919, 1921; Hoh River, 13363.

Buellia badioatra (Floerke) Koerb. — On rocks, talus slope, Olympic Hot Springs, 2101; Storm King Mountain at 3,500 ft., 2225; Boulder Peak at 5,500 ft., 2863, 2895.

Buellia papillata (Sommerf.) Tuck. — On soil, Steeple Peak at 5,500 ft., 2325.

Rinodina hallii Tuck. — On alder, Cape Flattery, 1905, 13138, 13141.

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NEW AND UNUSUAL AGARICS FROM MICHIGAN. III *

ALEXANDER H. SMITH

DURING late August and early September, 1940, heavy rainfall and moderately cool weather brought out a very luxuriant agaric flora in the vicinity of Ann Arbor. Fleshy forms were particularly abundant. The number of species of Tricholoma which appeared was greater than that seen during any previous season I had spent in Michigan. Species of Entoloma were also plentiful. *Entoloma prunuloides* was found in several localities in such quantity that one could have collected a truck load of it had he so desired. *Tricholoma resplendens, T. sejunctum,* and *T. transmutans* occurred everywhere throughout one large oak woods and were common in several other localities. The fleshier lignicolous species were no more frequent than usual.

Critical studies of nine species of Tricholoma, two of Lepiota, and one of Armillaria are included in this account. The collections cited have been deposited in the University of Michigan Herbarium. All color terms within quotation marks are taken from R. Ridgway, *Color Standards and Color Nomenclature,* Washington, D.C., 1912.

List of Species

Armillaria Ambrosii Bres. — Pileus 1–3.5 cm. broad, convex or with a slight umbo, sometimes obtusely conic, surface dry and densely covered by small granulose warts or scales or by a more or less even powdery covering (when the scales have been worn down or broken), surface even or slightly radially rugose, color white to whitish, becoming "cartridge-buff" at times, margin beautifully appendiculate with submembranous patches of the broken veil, the outer side of these patches bearing small powdery scales similar to those on the pileus; flesh white, thick on the disc,

* Papers from the Herbarium of the University of Michigan.

thin toward the margin, firm, dry; lamellae close (35–39 reach the stipe), broad (3 mm. ±), slightly but sharply adnexed, white, edges crenulate; stipe 5–7 cm. long, 2.5–3 mm. thick, equal above a base enlarged by adhering white mycelium and débris, increasingly granulose-scaly up to the apical submembranous annulus, white and silky above, glabrescent and merely faintly powdery in age, stuffed, concolorous with the pileus at all stages; annulus with powdery scales on under side, upper surface silky; spores 4 5 × 3 μ, hyaline, ellipsoid, smooth, amyloid; basidia four-spored; pleurocystidia and cheilocystidia not differentiated; gill trama homogeneous, nearly hyaline in iodine (basidia yellow); pileus trama homogeneous beneath a surface layer of globose thin-walled hyaline cells 20–35 μ thick, all parts yellowish in iodine or remaining nearly hyaline.

Gregarious under pine, Ogemaw Forest, Midland, Sept. 25, 1938 (11091).

I have found this species but once, and was then inclined to regard it as an albino form of *Armillaria rugoso-reticulata*. If, however, one adheres to the principle of using color to separate species in this group, Bresadola's species should also be recognized. On such a basis it is very close to the European *Cystoderma charcharias* or *Lepiota charcharias*, depending upon which name is preferred, but differs in being white. Both have amyloid spores, a character also possessed by the specimens of *A. rugoso-reticulata* in the University of Michigan Herbarium.

Lepiota cystidiosa, sp. nov. (Pls. I II). — Pileus (2) 3–9 cm. latus, conicus vel convexus, demum umbonatus vel planus, siccus, pulveraceo-squamulosus vel granulosus, pallidus, demum alutaceus; lamellae confertae, latae, albidae demum alutaceae; stipes 4–8 cm. longus, 3–7 cm. crassus, aequalis vel subbulbosus, dense pulverulentus; sporae 4–4.5 × 2.5 μ; pleurocystidia et cheilocystidia similia, 25–42 × 12–7 μ, distinctissima. Specimen typicum legit A. H. Smith n. 15268, prope Ann Arbor, Mich., Sept. 9, 1940; in Herb. Univ. Mich. conservatum.

Pileus (2) 3–9 cm. broad, obtusely conic to convex when young, becoming broadly convex to plane in age or occasionally remaining umbonate, the margin sometimes undulated or wavy, surface dry, at first covered by conic powdery warts from the disc to the margin, soon becoming merely granulose to pulverulent as the

warts break up, not truly scaly, the warts or powdery débris "pinkish buff" to "pale pinkish buff," the white flesh showing until late maturity, eventually somewhat brownish buff over all or "wood-brown," occasionally nearly glabrous in age, margin at first delicately appendiculate with soft powdery masses of veil tissue which soon fall off; flesh soft and dry, white, slowly changing to sordid buff (not reddish) when cut or bruised, odor sharp but faint and easily overlooked, taste bitterish; lamellae free but almost touching the stipe, broad (8–12 mm.), broadest at the stipe and tapering evenly to the margin, very close but distinct, 2–3 tiers of short individuals, pure white at first, soon cream-color and becoming "wood-brown" (dull brown) like the pileus, often stained dark sordid brown and in decaying pilei occasionally dark purple-brown overall; stipe 4–8 cm. long, 3–7 mm. thick, equal or the base slightly bulbous, hollow, rather fragile, context silky, surface over lower three fourths covered by dense powdery masses of veil tissue (up to the powdery zone left by the broken veil), silky over the upper portion, annulus seldom formed or soon evanescent, veil remnants concolorous with the powdery covering of the pileus, whitish beneath but in age generally "wood-brown" like the cap; spores 4–4.5 × 2.5 μ, ellipsoid or the base slightly truncate, hyaline, smooth, pale yellowish to tawny-brown in iodine; basidia four-spored; pleurocystidia abundant, usually fusoid with acute apices or ventricose-subcapitate, the head 3–5 μ in diameter, in water mounts usually with a slight incrustation and a highly refractive globular content (probably of oil droplets), 25–42 × 7–12 μ (or 20–30 × 8–12 μ in saccate individuals); gill trama homogeneous, nearly hyaline in iodine; pileus trama homogeneous beneath a surface covering of inflated, thin-walled cells 15–40 μ thick, which are tinged pale cinnamon in iodine-chloralhydrate solution.

Scattered on muck soil under a dense growth of Impatiens, Ann Arbor, Sept. 9, 1940 (15268). My first collection of this species was made on Sept. 23, 1931, at Cascade Glen, Ann Arbor. Since that time until 1940 I had searched in vain for enough material to study critically. Collection 15268 consisted of two market baskets full of fruiting bodies. The pleurocystidia were a constant character in No. 15268, as well as in No. 15217, from

Milford, Aug. 30, and in No. 15263, from Cascade Glen, Ann Arbor, Sept. 6, 1940.

I was at first inclined to place my collections in *Lepiota Hetieri*, but Kühner (1), who has published an account of that species, does not mention any pleurocystidia in his rather detailed description of the microscopic characters. In addition to this, there appears to be a difference in habitat, size, and color change. My specimens were in perfect condition, but did not show any tendency to stain red in any part until decay had set in, at which time the gills became spotted by very dark sordid purplish spots and finally turned purplish overall. Smith and Hesler (4) collected a fungus in the Great Smoky Mountains National Park which did show the color change to red when bruised and which has scattered pleurocystidia. We placed these specimens in *L. rufescens* because of their resemblance to Lange's (2) figures and because his description covered our specimens very well. Lange described the cystidia as being on the gill edge. Because pleurocystidia were rare in our specimens it appeared to me that Lange had probably overlooked them. It must be remembered that he was under the impression that pleurocystidia were not present in any of the Lepiotae, and therefore his data on this point cannot be given much weight. Kühner (1) has included several species with distinctive pleurocystidia in his treatment of the genus for France. Both Kühner and Lange compare *L. rufescens* to *L. rosea* Rea and apparently regard *L. rufescens* as varying considerably toward the rose or red color. This is not true for *L. cystidiosa*. If the *L. rufescens* of Lange does have pleurocystidia, then it and *L. Hetieri* are very likely distinct, but *L. cystidiosa* would still be distinct from either. Consequently it is described here as a new species.

Lepiota roseotincta, sp. nov. — Pileus 2.5–3 cm. latus, obtusus vel subconvexus, siccus, roseo-fibrillosus, tactu aurantius et demum fuscus; lamellae confertae, latae, albidae vel incarnato-tinctae, non maculosae; stipes 3–4 cm. longus, 4–5 mm. crassus, subclavatus vel anguste fusiformis, cavus, albidus, tactu aurantius et demum fuscus; sporae 7–10 × 4–5 μ. Specimen typicum legit A. H. Smith n. 15327, prope Ann Arbor, Mich., Sept. 13, 1940; in Herb. Univ. Mich. conservatum.

Pileus 2.5–3 cm. broad, convex or with a flattened disc, surface

dry, appressed-fibrillose, disc "deep Corinthian red," the marginal area streaked with "Corinthian pink" fibrils (deep to light pinkish-vinaceous), the ground color white, the fibrils arranged in appressed fascicles near the margin, not scaly, surface quickly staining bright orange when bruised, portions soon becoming blackish; flesh thin, white, soft, unchanging, odor none, taste mild; lamellae close to crowded, moderately broad, free, reaching the stipe (but tending to become remote in age), 1–2 tiers of short individuals, not staining when bruised, white or evenly flushed pink toward the margin of the pileus, edges even; stipe 3–4 cm. long, 4–5 mm. thick at the apex, slightly clavate-bulbous but tapered to a long point below (almost fusiform in one), hollow, fragile, white within, surface white and delicately white-tomentose above and below the median white membranous annulus, annulus with scattered, pink fibrils on the under side, surface fibrils both above and below the annulus quickly staining reddish orange when bruised, the stains eventually becoming sordid brown; spores narrowly subovoid, with an oblique apiculus and a somewhat pointed apex, 7–10 × 4–5 μ, smooth, turning rusty brown in iodine; basidia four-spored; cheilocystidia abundant, forming a sterile band along the edge of the gill, hyaline (in water or KOH), smooth, fusoid-ventricose with obtuse apices, 36–48 × 9–14 μ; pleurocystidia not differentiated; gill trama homogeneous, hyaline to pale yellowish in iodine; pileus trama homogeneous beneath an irregular layer of more or less radially arranged hyphae having sordid reddish contents in KOH and measuring 8–15 μ thick, the tissue beneath composed of hyaline hyphae of about the same diameter or slightly larger.

Gregarious on débris at the base of a basswood tree, Ann Arbor, Sept. 13, 1940 (15327). Known only from the type collection.

In many respects this species resembles *L. rubrotincta* Pk. It differs markedly from that species, however, in the very pronounced and rapid color change. As in *L. flammeotincta*, this change is confined to the surface fibrils of the pileus and stipe, but it is unlike that species in that the bruised portions darken in a short time and never regain their original color. The lamellae are merely flushed with pink and do not stain or exhibit any distinctive color change. *L. roseotincta* reminds one a lot of *Agaricus diminutivus* in its colors and the fibrillose surface cover-

ing of the pileus. Among the European species *L. sublittoralis* Kühner is apparently close, but lacks the striking color change.

Tricholoma aromaticum Murr. (Pl. III). — Pileus 3–7 cm. broad, obtuse with an inrolled margin when young, plane or umbonate in age, umbo obtuse, surface dry and unpolished, appearing glabrous to the naked eye and matted-fibrillose under a hand lens (10 ×), color evenly "tilleul-buff" (pallid) or slightly darker (color not well matched in R.), sometimes the margin "tilleul-buff" and the disc darker grayish buff, surface occasionally pitted or with brownish glabrous spots; flesh thick, firm, brittle, whitish, unchanging, odor and taste both strongly farinaceous; lamellae crowded and narrow (5–7 mm. at the base, which is the broadest point), rather sharply adnexed, 3–4 tiers of short individuals, color evenly "cartridge-buff" (pale sordid yellowish buff at maturity), near "tilleul-buff" when young but slightly paler than the pileus, edges slightly crenulate at times and even (not eroded); stipe 4–8 cm. long, 9–13 mm. thick, equal or a bit enlarged at the base, solid but becoming hollow, firm whitish and coated with appressed fibrils up to the almost cottony-pruinose apex, somewhat glabrescent where handled, veil not present; spores 4–5.5 × 2.5–3 μ, ellipsoid, smooth, hyaline, not amyloid; gill trama homogeneous, of narrow parallel hyphae, yellowish in iodine; pileus trama homogeneous, surface hyphae slightly narrower than the rest, all parts yellowish in iodine.

Gregarious under oak and aspen, La Badie Lake, near New Hudson, Oakland Co., Sept. 23, 1940 (15440).

The very small spores are the most outstanding feature of this species which can be clearly set forth in a description, but the fungus has a very striking appearance in spite of its pale colors. The very pale buff cap and yellowish gills both have a glaucous sheen not soon forgotten.

Its relationships are difficult to establish. In some respects the species resembles *T. sulphureum*, but the small spores and farinaceous odor are not in line with the members of that group. The appearance of the pileus reminds one of *T. acerbum* or *T. impolitum*, but it has more of a sheen than either. *T. Georgii* has the small spores, according to Ricken (3), but is smooth and glabrous. *T. albellum* sensu Rea is apparently very close. Rea describes the spores as 5–6 × 3 μ. My specimens were not scaly

in any sense of the word. The very thin appressed-cottony covering over the entire stipe is an outstanding feature not mentioned in descriptions of European species. Toward the apex of the stipe this layer becomes thinner and frequently breaks up, giving the impression of a soft pruinose coating.

The specimens of No. 15440 have only a slight pungent odor in the dried condition, and no odor is now present in the type. It thus appears that in this instance the choice of the specific name was most unfortunate. I did not find the spores of the type measuring more than 5.5 μ long; 4–5 $\times$ 2.5 was the usual size in my collection.

Tricholoma cuneifolium (Fr.) Gillet. — Pileus (1) 2.5–5 cm. broad, obtusely conic when young, soon convex or with an obtuse conic umbo, sometimes broadly campanulate, margin inrolled at first, surface moist and hygrophanous, evenly "fuscous" (dark to pale cinereous), the disc often remaining darker, atomate when faded, not striate at any stage, surface often having a hoary sheen when moist; flesh thick under the disc (3) 6–8 mm., tapered abruptly toward the margin, very fragile and brittle, pale grayish, becoming pallid, unchanging, odor and taste farinaceous; lamellae close (45–52 reach the stipe), 2–3 tiers of short individuals, broad and decidedly ventricose at maturity (up to 1 cm. broad), adnexed, whitish to pale gray, edges even or eroded; stipe 3–8 cm. long, 3–8 mm. thick, equal or narrowed at the base, solid, white both inside and out, glabrous, unchanging when cut or bruised, fleshy and very brittle; spores 5–6 $\times$ 3 μ, narrowly ellipsoid, smooth, not amyloid; basidia four-spored; cheilocystidia and pleurocystidia not differentiated, gill trama subparallel, yellowish to hyaline in iodine; pileus trama composed of a palisade of more or less upright pear-shaped cells 32–60 $\times$ 9–20 μ and with dull fuscous brown walls when revived in KOH, tramal body of hyaline hyphae which turned yellowish in iodine.

Single to gregarious on rich humus, 1940: Ann Arbor, Sept. 6 (15261); Sept. 11 (15549); Sept. 13 (15351); Sharron Hollow, Sept. 14 (15369); Ann Arbor, Sept. 16 (15416); La Badie Lake, New Hudson, Oakland Co., Sept. 23 (15445) and Sept. 24 (15459).

Most of the collections consisted of only one or two small

fruiting bodies, but all were saved because of the interesting microscopic characters. The species was widely distributed about Ann Arbor during the season of 1940, but was certainly not abundant. I had almost despaired of finding sufficient material for a critical study. It has a superficial resemblance to *Collybia hymenocephala* in color and in the anatomy of the pileus. The amyloid reaction of the spores of *C. hymenocephala* at once distinguishes dried material, and the stature readily separates fresh specimens. My collections have been compared with specimens of *T. cuneifolium* sent by M. Josserand, Lyon, France, and appear to be the same. Large fruiting bodies dry a darker gray than the specimens from France, which were smaller than most of mine. My smallest specimens, however, dried paler than the larger ones and are similar in color to those from Josserand. The farinaceous odor and taste separate large specimens from *T. atrocinereum.*

Tricholoma fallax (Pk.) Sacc. — Pileus (0.5) 1–3 cm. broad, very broadly convex to obtusely umbonate and with an incurved margin when young, expanding to plane and frequently developing a recurved margin, the umbo usually disappearing, glabrous, moist, lubricous, and soft, "ochraceous orange" to "ochraceous tawny" when moist, fading to "light orange-yellow" and appearing somewhat canescent when faded, hygrophanous to subhygrophanous, glabrous, no veil remnants seen; flesh moderately thick under the disc and tapering abruptly toward the margin, soft, near "old gold" when moist, pale yellowish when faded (often concolorous with the surface when moist), odor none, taste mild; lamellae crowded, 24–27 reach the stipe, 3 tiers of short individuals, narrow to moderately broad (2–2.5 mm.), broadest at the base and usually sharply adnexed, evenly "light orange-yellow" when young but developing a whitish pruinose sheen (probably from the spores), edges even; stipe 2–3.5 cm. long, 3–4 mm. thick, usually enlarged toward the apex, base inconspicuously fibrillose, coated with appressed yellowish fibrils overall but somewhat glabrescent in age, concolorous with the lamellae above, darker sordid yellowish below, solid but developing a tubule; spores 3–4 × 2.5 μ, hyaline, ellipsoid, smooth, not amyloid; basidia four-spored, 18–20 × 5–6 μ; cheilocystidia and pleurocystidia not differentiated; gill trama homogeneous, cells

with yellow contents in water mounts of fresh material, yellowish in iodine; pileus trama homogeneous beneath a palisade of clavate to pear-shaped cells 18–25 × 8–10 μ, which have thin walls and bright yellow contents, the hyphae of the tramal body also with yellow contents, all parts yellowish in iodine.

In arcs on humus under oak, Milford, August 30, 1940 (15214). The description was drawn from this collection. I found the fungus twice in Oakland County during August, 1937, and have collected it under conifers in Nova Scotia, Ontario, northern Michigan, Washington, Oregon, and California. Kauffman collected it in New York.

Through the kindness of Dr. H. D. House, New York state botanist, I have been able to study the microscopic characters of Peck's type. The pileus is corticated by a palisade of cells as described above, and the other characters also check with those given in the description above. Kauffman left three collections identified as *T. fallax:* two from the Adirondacks and one from Colorado. In the collection dated September 7, 1914, from the Adirondacks, the pileus is perfectly homogeneous; in the other from this locality, dated September 9, 1914, the pilei are corticated. The habitat of the second collection is not recorded; that of the first is given as "under spruce and balsam." The third collection, made in 1920, consists of fruiting bodies with homogeneous pilei. It is evident from Kauffman's New York material that both species look just about alike, and very likely they grow in the same habitats. Habitat must be ruled out as a distinguishing character here because I have found typical *T. fallax* in forests of both types.

The discovery that *T. fallax* belongs in the subgenus Dermoloma and that a second species exists which has the same appearance brings up the problem of a name for the second one and raises the question whether *T. fallax* occurs in Europe. Lange has described two species of this general type, but has not classified either one in Dermoloma. Consequently the validity of his use of the name *T. fallax* must now be checked before it can be accepted. A study of the dried specimens would quickly settle this question. The name to be used for the species with the homogeneous pileus remains a problem and involves the names *T. cerinum, T. pseudoflammula,* and *T. chrysenterum.*

Murrill changed the specific name of Peck's species and made the combination *Melanoleuca naucoria* because of the existence of *Agaricus fallax* Lasch, published before Peck's name. Both applied to species of Tricholoma. Lasch's species, however, was referred to *T. ionides* by Fries, and the combination *T. fallax* (Lasch) was apparently not published. Saccardo published the combination *T. fallax* (Pk.), thus validating Peck's name in the genus Tricholoma.

Tricholoma huronense, sp. nov. (Pls. IV–V). — Pileus 6–9 (12) cm. latus, obtusus, demum subumbonatus vel planus, siccus, fibrillosus demum cinereo-squamosus, caro albida; lamellae confertae, angustae demum sinuatae, sordide albidae; stipes 4–8 cm. longus, 1–2 cm. crassus, clavatus, solidus, albidus, deorsum cinereo-squamulosus, sursum albido-fibrillosus et rubro-guttulatus; sporae 7–9 × 5–6 μ. Specimen typicum legit A. H. Smith n. 15303, prope Ann Arbor, Mich., Sept. 11, 1940; in Herb. Univ. Mich. conservatum.

Pileus 6–9 (12) cm. broad, gibbous when young or evenly obtusely conic with an incurved margin, becoming convex and finally plane or with a low obtuse umbo, surface dry and fibrillose, "drab-gray" to "pale smoke-gray" when young (pale to moderately dark cinereous), the fibrillose gray cuticle soon becoming broken up into appressed drab spotlike scales around the disc, the white flesh showing through along the margin, margin at maturity or in age often appearing white streaked with gray fibrils, or with appressed-fibrillose patches, the margin slightly fringed and somewhat cottony but no cortina visible on buttons as small as 3–6 mm., often beaded with drops of a clear pink fluid or streaked pinkish along the margin in either young or old pilei; flesh thick and white, not changing color when cut or bruised, odor and taste both distinctly farinaceous; lamellae close to crowded (96–115 reach the stipe), adnexed, rather narrow, equal (4–8 mm.), 2–3 tiers of short individuals, dull white (more cream-color than the flesh), edges slightly eroded, not staining when bruised or broken and not discoloring appreciably in drying; stipe 4–8 cm. long, 1–2 cm. thick at the apex, solid, clavate and 2–4 cm. thick at the base, fleshy, white within, surface whitish but covered over the lower portion by appressed-fibrillose scales similar to those on the pileus, scales very pale when young but

darkening in age, silky toward the apex, often beaded with hyaline or pinkish drops of fluid or with pinkish streaks, base sometimes stained ochre-yellow, but no such color change evident when cut or bruised; spores smooth, ellipsoid, 7–9 × 5–6 μ, not amyloid; basidia four-spored; cheilocystidia 28–39 × 6–12 μ, saccate to somewhat fusoid-ventricose, when revived in KOH slightly yellowish as seen in mass on the gill edge; gill trama and pileus trama both yellowish in iodine and homogeneous.

Gregarious to caespitose in arcs in oak woods, Ann Arbor, Sept. 11, 1940 (15303).

A truck load of this species could have been collected in one locality on September 11. It was found in smaller amounts in many other local areas during the season of 1940, and the reddish drops of liquid were always present. The yellowish stains at the base of the stipe, however, were not constant. The strong farinaceous odor and taste, pale gray color, scaly cap, rather broad spores, and red drops distinguish it from all other species.

No cortina was observed on any of the numerous young pilei. The scales on the stipe are apparently formed by the surface fibrils becoming aggregated into patches. The fibrillose layer covering the surface of the stipe is of a very loose texture. The scales darken in age in much the same manner as those on the stipes of fruiting bodies of *Hygrophorus tephroleucus*. Specimens in which this color change does not take place, and in which the color of the pileus has faded, are almost indistinguishable from *T. venenata*. The gills of the latter, however, become brownish in age. *T. huronense* is most closely related to the species in the *T. terreum* group.

Tricholoma luteomaculosum, sp. nov. (Pl. VI). — Pileus 4–10 cm. latus, obtusus demum late convexus vel subplanus, siccus, fibrillosus vel squamulosus, saepe rimosus, caeruleo-griseus vel obscure cinereus; caro tactu luteo-maculata; lamellae confertae, latae, sinuatae, saepe lutescens, acie saepe cinerescens; stipes 4–8 cm. longus, 1–2 cm. crassus, aequalis, farctus demum cavus, pallidus, tactu luteo-maculosus; sporae 5.5–7 × 4–5 μ. Specimen typicum legit A. H. Smith, n. 15447, prope Ann Arbor, Mich., Sept. 27, 1940; in Herb. Univ. Mich. conservatum.

Pileus 4–10 cm. broad, obtuse when young, becoming broadly convex or nearly plane at maturity, the margin sometimes ele-

vated and wavy, often cracking or splitting radially to the disc, surface dry, glabrous to minutely fibrillose near the margin or with very small appressed or slightly recurved scales over the marginal area, disc appearing glabrous but somewhat streaked and, under a lens, innately fibrillose, occasionally the disc also with very minute blackish scales, color "Quaker-drab" to "pallid mouse-gray" (dark to light bluish gray), disc darker than the margin but not blackish gray; flesh thick, brittle, grayish to drab in the upper part, whitish near the gills, staining pale greenish yellow when bruised, at times the entire cap tinged greenish yellow (usually in age), taste farinaceous, odor slightly farinaceous; lamellae close, broad, adnexed, whitish to pale cinereous, staining pale greenish yellow when bruised (stain very pronounced in fresh young specimens), edge eroded and sometimes staining blackish; stipe 4–8 cm. long, 1 2 cm. thick, equal or the base slightly enlarged, white or tinged pale grayish, innately fibrillose, no cortina evident, stuffed but becoming hollow, flesh changing to yellowish green when bruised, base white-cottony with adhering mycelium; spores 5.5–7 × 4–5 μ, smooth, ellipsoid, not amyloid; basidia four-spored; cheilocystidia abundant, saccate, fusoid or fusoid-ventricose, 36–52 × 12–18 μ, apices obtuse or acute; pleurocystidia rare to scattered or fairly abundant, saccate to flask-shaped, often ovoid above a narrowed pedicel, 36–40 × 10–15 μ, scarcely projecting from the hymenium, smooth; gill trama and pileus trama both yellowish in iodine and homogeneous.

Gregarious on humus in oak woods, Ann Arbor, Nov. 4, 1936 (6166), and Sept. 27, 1940 (15447).

The bluish gray to dull ash-gray pilei which may become slightly scaly, the lack of a cortina, the pronounced change in color to greenish yellow when the flesh of young pilei is bruised, and the presence of pleurocystidia in addition to the cheilocystidia distinguish this species.

I was at first inclined to identify my collections as *T. scalpturatum* Fr., but in specimens of that species from M. Josserand no pleurocystidia were found, and the cheilocystidia were scarcely differentiated. In addition, if one goes back to the Friesian descriptions, certain discrepancies in the macroscopic characters are apparent. *T. scalpturatum* grows in grassy places under fir in

the mountains, the scales of the pileus become somewhat reddish, and the gills are yellowish only in age or when dried. These characters are in direct contradiction to those observed on the Michigan material. The absence of a cortina in my specimens may also be significant, but that is a character which might be very easily missed and which might vary from year to year.

Tricholoma michiganense, sp. nov. (Pl. VII). — Pileus 5–9 cm. latus, obtusus vel convexus, demum subumbonatus, siccus, squarrose squamulosus vel lacerate squamulosus, atro-cinereus; caro alba, tactu rubescens, odore et sapore distinctissimis; lamellae confertae, angustae, cinereae demum pallidae, incarnato-maculatae; stipes 3–8 cm. longus, 10–12 mm. crassus, aequalis vel subaequalis, solidus, intus obscure cinereus demum pallidus, fusco-fibrillosus; cortina nulla; sporae 6–7 × 3–3.5 μ. Specimen typicum legit A. H. Smith n. 15441 prope New Hudson, Oakland Co., Mich., Sept. 24, 1940; in Herb. Univ. Mich. conservatum.

Pileus 5–9 cm. broad, convex to obtuse, expanding to plane or with a low obtuse umbo, margin remaining inrolled for a long time, surface dry and minutely squarrose scaly to lacerate-scaly over the marginal area, disc with matted fibrils, color "fuscous" to "hair-brown" over the disc and on the scales, the whitish flesh showing through the fuscous fibrillose surface covering only near the margin, in age the surface fibrils becoming "drab-gray," the flesh beneath becoming tinged with pale salmon color; flesh thick over the disc, firm, pallid at maturity, pale drab in very young individuals, becoming tinged orange-salmon color in age or when bruised (reaction tardy in some specimens or may not be evident at times), odor similar to that of *Tricholoma sulphureum* but fainter, taste very disagreeable and tardily subacrid; lamellae crowded, narrow (5 mm. ±), many tiers of short individuals present (as in Melanoleuca), rounded-adnexed, pale drab in young caps, slowly becoming whitish and in age stained pale salmon color, edges even; stipe 3–8 cm. long, 10–12 mm. thick above a narrowly clavate base, solid, fleshy, pale drab within at first, whitish in age, surface covered to the apex with "fuscous" fibrils which become more or less torn into lacerated scales, base surrounded by a whitish mycelium which becomes pinkish when bruised; spores 6–7 × 3–3.5 μ, ellipsoid, not amyloid; basidia

four-spored; cheilocystidia filamentose, rare; pleurocystidia not differentiated; gill trama and pileus trama both yellowish in iodine and homogeneous.

Scattered on muck soil or around oak stumps on rich humus, La Badie Lake, New Hudson, Oakland Co., Sept. 23 and 24, 1940 (15441, type, and 15465).

One of the most curious features of this fungus is that, if one moistens a fragment of the pileus of a dried specimen and then crushes it between his fingers, the odor of coal tar is readily detected, and, in fact, is more pronounced than in the fresh material. Whether this character will disappear with age I am not prepared to say, but it is unique so far as my experience with the genus is concerned. The flesh did not change color readily in the specimens of collection 15465, but did so very readily in the other. I have found occasional specimens of *T. orirubens* which also did not change color readily, and I consider this tardiness to be a variation within the species.

The outstanding characters of *T. michiganense* are the drab colors of pileus and stipe, scaly cap, lack of a cortina (although the pileus may bear a fringe of fibrils along the margin), the color change, and the odor. I examined buttons in which the margin of the pileus touched the stipe, but in no case was there evidence of a veil. The margin is incurved and the fibrils of the surface of the pileus merely project beyond the incurved margin into the gill cavity. The gray fibrillose covering of the stipe extends up to the gills and appears to be independent of the covering of the pileus. This is an unusual situation in a species in which both the pileus and the stipe are scaly and the scales similarly colored.

T. michiganense clearly belongs among the scaly species of the *T. terreum* group and apparently is quite similar in appearance to *T. atrosquamosum.* Both the odor and the taste should separate it at once from that species even if the incarnate tint fails to develop. *T. orirubens* is distinguished not only by a different taste and odor but also by the lack of a covering of gray fibrils over the stipe.

Tricholoma palustre, sp. nov. — Pileus 4–8 (9) cm. latus, late convexus demum planus vel subdepressus, siccus vel subudus, griseo-olivaceus vel olivaceus, ad marginem luteo-olivaceus;

sapor intense acris; lamellae confertae, sinuatae, latae, pallide luteo-olivaceae; stipes 5–6 cm. longus, 1–1.8 cm. crassus, aequalis, farctus demum cavus, pallidus vel olivaceo-tinctus, intus albidus; sporae 5–6 × 4–5 μ. Specimen typicum legit A. H. Smith n. 15471 prope New Hudson, Mich., Sept. 25, 1940; in Herb. Univ. Mich. conservatum.

Pileus 4–8 (9) cm. broad, very broadly convex with an inrolled margin when young, becoming plane at maturity or remaining broadly convex, occasionally shallowly depressed over the disc and the margin arched, surface moist to dry, appearing matted-fibrillose under a lens, not sticky to the touch, color near "olive-buff" (pale yellowish olive), sometimes "pale chalcedony-yellow" on the margin (very pale yellow with only a trace of green), more grayish olive toward the disc, which is sometimes dirty gray to brownish gray (color persistent in dried material), the gray color apparently being caused by a discoloration of the surface fibrils; flesh thick on the disc, firm, white, grayish just beneath the cuticle, odor none, taste mild at first and not at all farinaceous, tardily becoming very sharply acrid; lamellae broad (10–12 mm.), close to crowded, rather sharply adnexed, "pale chalcedony-yellow" to "olive-buff" (almost concolorous with the olive-colored parts of the cap), the edges very eroded; stipe 5–6 cm. long, 1–1.8 cm. thick at the apex, equal, firm, stuffed, becoming hollow, white within, the exterior whitish or only with a very faint tinge of olive, glabrous to faintly appressed silky-fibrillose, not scaly; spores 5–6 × 4–5 μ, not amyloid, broadly ellipsoid to subglobose, smooth; basidia four-spored; cheilocystidia scattered to rare, saccate and 9–12 μ broad or merely resembling immature basidia; gill trama homogeneous beneath a thin scarcely differentiated pellicle of olive-green nongelatinous hyphae only slightly narrower than those of the tramal body.

Scattered on humus at the edge of a bog, La Badie Lake, New Hudson, Sept. 23 (15450), and Milford, Sept. 25, 1940 (15471, type).

T. palustre was found growing with *T. acre* Pk. on wet marshy soil at the edge of a bog. It is practically identical with *T. acre* in taste, stature, and the appressed fibrils on the surface of the pileus. In wet weather both species may appear moist, but they are properly classified near *T. virgatum*. The olive color at once

distinguishes *T. palustre* from all other species in this group. As in *T. sejunctum*, the amount of gray present over the disc may vary greatly depending directly, of course, on the amount of discoloration the surface fibrils undergo.

Tricholoma subcerinum, sp. nov. — Pileus 3–5 cm. latus, planus vel umbonatus, glaber, subhygrophanus, alutaceus demum avellaneus; caro aquosa; lamellae confertae, adnatae vel subsinuatae, angustae, subcerinae demum pallide alutaceae; stipes 3–4.5 cm. longus, 6–8 mm. crassus, cavus, aequalis, impolitus; sporae 3.5–4 × 2 μ. Specimen typicum legit A. H. Smith n. 6286, prope Milford, Mich., June 11, 1936; in Herb. Univ. Mich. conservatum.

Pileus 3–5 cm. broad, plane to slightly umbonate, the margin inrolled, glabrous, moist and watery, "snuff-brown" or slightly paler (dull yellowish brown), subhygrophanous, fading slowly to dull or grayish avellaneous, opaque at all times; flesh soft, watery, concolorous with the pileus both when moist and when faded, thickish, odor none, taste slightly bitterish; lamellae crowded, adnate to sinuate, narrow, "cartridge-buff" when young (very pale yellowish buff), in age nearly concolorous with the pileus, edges even; stipe 3–4.5 cm. long, 6–8 mm. thick, hollow, fleshy-tough, fibrous, equal, surface toward the apex dull or faintly pruinose, unpolished over the remainder, base white-mycelioid, not scaly in age; spores minute, 3.5–4 × 2 μ, ellipsoid, hyaline, smooth, not amyloid; basidia four-spored, 14–16 × 4–5 μ; cheilocystidia and pleurocystidia not differentiated; gill trama homogeneous, yellowish in iodine; pileus trama homogeneous beneath a palisade layer of hyaline pear-shaped cells 15–20 × 8–10 μ, the remainder filamentose and yellowish in iodine.

Scattered on muck at the edge of a bog, Milford, June 11, 1936 (6286).

Although larger, this species is similar to *T. fallax* both in having a palisade of upright pear-shaped cells over the pileus and in its very minute spores. It differs in its much duller colors and in having the stature of *T. melaleucum*. From species of the subgenus Melanoleuca it is at once distinguished by its smooth nonamyloid spores and lack of cheilocystidia.

Peck's description of *T. Thujinum* reads very much like that of *T. subcerinum*. The type, which has been examined, differs in lacking the palisade of upright cells over the pileus. Through

the kindness of Dr. H. D. House I obtained material for a study of the microscopic details. The pileus was found to be homogeneous, the spores smooth, minute (as Peck described them), and not amyloid. No pleurocystidia or cheilocystidia were seen. The subhymenium was rather rusty brown when revived, but this may have been due to the age of the material and the way it was dried. The basidia are very small (15–18 × 3–4 μ).

It is quite apparent that here we have a situation similar to that discovered for *T. fallax*. Two species with very much the same appearance differ sharply in the structure of the surface layer of the pileus.

Tricholoma venenatum Atk. — Pileus (3) 5–9 (11) cm. broad, obtuse to broadly convex when young, expanding to umbonate or plane, the umbo when present broad, the margin often becoming arched or elevated and somewhat wavy, sometimes the margin furrowed in young specimens, surface dry, appressed-fibrillose at first, in age the fibrils becoming aggregated into appressed scales, the scales and fibrils becoming pale sordid brownish ("pinkish buff" to "avellaneous") giving the disc a pale sordid avellaneous sheen; flesh thick, soft, only moderately fragile, white, slowly changing to pale buff but no typical change evident when bruised or broken, odor slightly farinaceous when flesh is crushed, taste bitter and subfarinaceous; lamellae rather close (74–80 reach the stipe), 2–3 tiers of short individuals, moderately broad (7–10 mm.), broadly and sharply adnexed, usually with a decurrent tooth, sometimes intervenose, white to cream-color at first, in age pale avellaneous, the edges a bit darker at times and usually slightly eroded; stipe 6–10 cm. long, 12–15 mm. thick at the apex, solid or hollowed by worms, flesh white, not changing when cut, equal or narrowly clavate, surface white overall, unpolished and obscurely fibrillose, discoloring slightly around the base or where handled (the appressed fibrils discolor as do those on the pileus); spores hyaline, 6–7 × 4–5 μ, smooth, not amyloid; basidia four-spored; cheilocystidia scattered to rare, saccate, smooth, 25–36 × 7–10 μ; pleurocystidia none; gill trama and pileus trama both yellowish in iodine and homogeneous.

Scattered to gregarious under brush in wet places on a hillside, Cascade Glen, Ann Arbor, D. E. Stuntz and A. H. Smith, July 3, 1940 (15171). I have collected this fungus repeatedly in this one

locality for over a period of years, but not until the season of 1940 did it fruit in sufficient quantity to justify a critical study.

The bitterish, somewhat farinaceous, taste has always been a constant character of the specimens from this locality, as has been the color change to brownish. Specimens from near Milford which in every other respect appeared to be identical with those mentioned above were mild in taste. Since the sum total of all other characters clearly points to the identity of the Ann Arbor specimens with Atkinson's species, it seems best in this instance to disregard taste as a character of major taxonomic importance. My detailed description of the bitter form of *T. venenatum* is intended to be compared with other accounts of the species and to aid in distinguishing between this form and *T. huronense*, to which it appears to be closely related and with which it could be confused.

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Lepiota cystidiosa Smith. × 1. Young specimens

Lepiota cystidiosa Smith. × 1. Old specimens

Tricholoma aromaticum Murrill. × 1

Tricholoma huronense Smith. × 1. Young specimens

Tricholoma huronense Smith. × 1. Old specimens

Tricholoma luteomaculosum Smith. × 1

Tricholoma michiganense Smith. × 1

PLEISTOCENE MOSSES FROM THE AFTONIAN INTERGLACIAL DEPOSITS OF IOWA *

WILLIAM CAMPBELL STEERE

INTRODUCTION

MOSSES and liverworts occur as fossils less frequently than any other large group of plants. The most important reason for their rare fossilization is their relatively delicate and fragile structure, caused by the lack of hard tissues or resistant materials in the walls of individual cells. Furthermore, the plants are small and inconspicuous and, consequently, extremely easy to overlook in fossil material. As a result, only a few traces of the undoubtedly well-developed bryophyte flora of past epochs have been discovered.

The few species of bryophytes which have been reported in a truly fossilized condition (Knowlton, 1902, 1919; Dixon, 1927) date, without exception, from pre-Pleistocene times and occur principally in Tertiary deposits. By far the great majority of fossil mosses thus far reported date from the Pleistocene or very shortly thereafter and are, strictly speaking, in only a subfossil or "humified" condition. Isolated fragments of leaves, branches, and stems have been found embedded in old river and lake silts, and whole plants have been discovered *in situ* in ancient peats and forest beds.

Comparatively little importance has previously been attached to the study of Pleistocene mosses in this country and, as a consequence, few species have been reported. In the glaciated parts of Europe, on the other hand, many accurate and significant studies have been made. The number of species of bryophytes which have been reported from Pleistocene or post-Pleistocene deposits amounts to the rather surprising total of well over three hundred, of which somewhat less than ten per cent are hepatics (Dixon, 1927; Gams, 1932).

In this country the majority of Pleistocene mosses have been reported, not from the most recent deposits, but from the most

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ancient interglacial deposits, a brief history of which follows (cf. Kay, 1924, 1929; Kay and Apfel, 1928).

After the retreat of the Nebraskan ice sheet, which, so far as is known, was the first to invade the Mississippi basin, and before the coming of the next or Kansan ice sheet, there was a long interglacial interval. Evidence of this is given by the widespread occurrence in Iowa and neighboring states of weathered sands and gravels, old soils and forest beds, and layers of peat and muck, which rest upon the Nebraskan drift, but which in turn are buried by the Kansan till sheet. Since these ancient soils and peat beds were first discovered and studied near Afton, Union County, Iowa, the first known interglacial interval, which probably began nearly a million years ago and lasted over a hundred thousand years (Leverett, 1930), was named "Aftonian." Subsequent to their original discovery and identification Aftonian deposits have been reported from nearly forty counties in all parts of Iowa, as well as in Missouri, Nebraska, South Dakota, Minnesota, Wisconsin, and Illinois. The deposits have been uncovered in excavations and gravel pits, in road and railway cuts, and have frequently been penetrated by wells, but are only rarely exposed in nature.

One of the most characteristic features of Aftonian deposits is the very common occurrence in them of large quantities of well-preserved mosses. As a result of earlier studies of Aftonian material several mosses are already known from various parts of Iowa. From Dodge Township in Union County (the type locality) have been reported *Camptothecium nitens* and *Drepanocladus fluitans* (Savage, 1903, 1905); from Oelwein in southern Fayette County, *D. fluitans* (Beyer, 1896; Macbride, 1896), *D. revolvens* and *Calliergon Richardsonii* (Holzinger, 1903); from Iowa City in Johnson County, *D. fluitans* var. *glaciale* (Holzinger, 1903); from Mud Lake, Emmet County, *D. fluitans* var. *Jeanbernati* (Grout, 1930); from Wallingford in Winnebago County, *Camptothecium Woldenii* (Grout, 1917). This last-named species is known only from this one locality, and is apparently now extinct. According to Dr. Grout, the species to which it is most closely allied (*C. pinnatifidum*) is not now found east of the Rocky Mountains.

In addition to the definite, well-authenticated records just cited many references to bryophytes exist in the literature concerning the Aftonian deposits. Since they are mentioned simply as "mosses"

or as occurring in "moss-bearing layers," it is impossible to determine what species are represented (Tilton, 1910, 1911; and others). In the geological surveys of the various counties of Iowa reports of ancient soils which bear mosses occur especially frequently.

In addition to the bryophytes from deposits which are almost certainly Aftonian there are reports of several species which somewhat doubtfully belong to that horizon. Under this heading come the Dichelyma from Bloomington, Illinois, which, although considered by Dr. T. P. James to be a new species, was not described as such because of its sterile condition (McGee, 1891); and *Drepanocladus aduncus* from Davenport, in Scott County, Iowa (Pratt, 1876).

An interesting collection of Pleistocene mosses was made in Minneapolis, Minnesota, from which have been reported *Calliergon giganteum;* a new species of Drepanocladus, *D. minnesotensis;* and a new genus, Neocalliergon, erected for *N. integrifolium* (Williams, 1930a, 1930b; Cooper and Foot, 1932). Although it is stated that this material came from deposits believed to date from late Pleistocene, the novelty of such a large part of it arouses a suspicion that they might possibly be Aftonian. Leverett (1932) remarks that Aftonian deposits have been found relatively close to the surface farther south in Minnesota. He says: "At several places in southeastern Minnesota and neighboring parts of Wisconsin and Iowa there are soils and beds of peat and muck between till sheets, which have been commonly referred to the Aftonian interglacial stage. Among the earliest brought to notice are those of western Fillmore County and southern Mower County, Minnesota, discussed by Winchell. As a rule the bed of muck and peat is found at the moderate depth of 20 to 30 feet. The greatest depth noted is 50 feet; the least is only 7 feet." "Another exposure of a peaty bed between tills is found in a cut on the Chicago, Rock Island & Pacific Railroad 2 miles southeast of Fairbault, Minn. Above the soil is 20 feet of bluish till . . . ."

Professor C. O. Rosendahl, of the University of Minnesota, has told me (*in litt.*, 1939) of collecting plants in deposits of Aftonian age in Minnesota, and I have seen mosses from these collections.

Other deposits which might possibly be relics of Aftonian times are those in the vicinity of Toronto, from which several species of mosses have been reported (Hinde, 1877; Dawson and Penhallow,

1890; Penhallow, 1896, 1900; Coleman, 1894, 1895). These deposits are so close to the gathering grounds of the ice sheets that much of the evidence for their position in the Pleistocene is lacking. Consequently it is exceedingly difficult or impossible to correlate exactly these deposits with those at the margin of the glaciated area.

Mosses which certainly date from interglacial stages in the Pleistocene later than the Aftonian have been reported from Ohio (Orton, 1870), Wisconsin (Cheney, 1930, 1931; Wilson, 1932, 1935, 1936), Minnesota (Winchell, 1888), Alaska (Cooper, 1923), District of Columbia (Williams, 1933), and Louisiana (Steere, 1938b).

The few records of fossilized postglacial mosses in North America occur principally from travertine or tufa deposits in Oklahoma (Emig, 1918) and Utah (Flowers, 1933).

MATERIAL

The material to be discussed here was collected in the type locality of the Aftonian interglacial stage near Afton, Iowa, during the summer of 1933. Since the collectors, Dr. Ethel B. Hansen and Dr. Gladys West, were primarily interested in the identification of the species of higher plants, the large collection of mosses was turned over to me for study.

The mosses occurred in thin layers in a clayey silt, which is clearly varved. They were not equally distributed through the whole section, which was several feet thick, but were highly localized. The layer in which they were most abundant was called by the collectors "Layer C," and from it came the great majority of the species listed in this paper. The thinness of the varves and the types of mosses preserved indicate the margin of an ancient boggy lake or a slow-moving bog stream.

The moss-containing fragments of clay were carefully washed in a sieve or strainer, to remove most of the dirt from the plant débris, which was then sorted. The mosses were received for study in this cleaned condition, but had not been given chemical treatment of any kind. The specimens were yellowish to clear reddish brown when wet, and so fragile that they could be handled only by small brushes. When dry, they were light, dusty brown and crumbled into fragments if touched.

In order to facilitate the study of the specimens each fragment of branch or stem was partially dissected to show all diagnostic de-

tails of the leaves necessary for identification, as, for example, their attachment to the stem and the cellular areolation of base and apex. The dissections were mounted in a dark glucose syrup ("Karo") under a glass cover slip. This technique for mounting fossil materials, which was originated many years ago by Professor H. H. Bartlett, results in hard, permanent mounts. In the thin layer under the cover glass the dark syrup is entirely transparent and appears colorless. The advantage of the dark syrup is that it never crystallizes, which is the greatest fault of water-glass or pure glucose-syrup mounts.

In general, the material is in remarkable condition, especially since it must have been carried about by water currents before being finally covered with silt. Many of the stems are exceedingly flattened, so that their cell structure and arrangement are not easily recognizable, and the apices of occasional leaves have been frayed or destroyed. Rarely, fungous hyphae are visible (Pl. V, Fig. 5). The wonderful preservation of mosses in Aftonian deposits, approximately a million years old, has excited considerable comment. Grout (1917) remarks upon the unusual condition of specimens of *Camptothecium Woldenii:* "The material is somewhat coated with fine soil, although Mr. Wolden says he washed it out from lumps of earth. Otherwise it might have been collected one hundred days ago instead of having been preserved one hundred thousand years, more or less. The plants are green, although no cell contents are observable, and the leaves are perfectly preserved, even to all details of cell structure. In fact it seemed so incredible that a moss could have remained so well preserved under such circumstances, that I wrote again to Mr. Wolden for additional details."

Professor Macbride (1896) gives an even more graphic (and extravagant) description: "The bottom of the seam is a compact mass of moss, compacted and pressed together no doubt, but absolutely untouched by putrefaction or decay, perfect in every leaf and fiber as any herbarium specimen in the world. Specimens you may examine show this perfectly. You may see the stem, the attachment of the leaves, the innovations, the form of each leaf, nay, the very areolation of a leaf apex and base, quite as absolutely defined as in the case of any freshest specimen one may bring in now from any living turf or forest bed. For this reason, we are able with much confidence to identify the species concerned, although, so far,

we have seen no smallest sign of capsule or fruit. So far, also, all the material seems to represent but a single species, a *Hypnum,* probably *Hypnum fluitans . . . .*"

In the following list of mosses which have been recovered from the Aftonian material collected by Dr. Hansen and Dr. West four species seem sufficiently distinct from their known modern relatives to deserve specific recognition, and so are here proposed as new species. Of course, there are widely divergent methods of considering the extent and limits of species in fossil material (Bailey, 1933), just as there are in the the study of modern plants. In modern bryology suitable and fairly satisfactory diagnostic criteria and concepts of specific boundaries exist, which, fortunately, can be readily adapted to Pleistocene material. It is difficult to agree with Gams (1932), however, who says somewhat arbitrarily: "None of the more experienced bryologists of today venture to create new Quaternary species of the polymorphic Amblystegiaceae, which seem to have existed in Europe almost unchanged since the Miocene." In the first place, the majority of species reported from Pleistocene deposits are known from the Tertiary in North America and, furthermore, many which are called preglacial are very probably really interglacial in age, but from outside the limits of glaciation, or else from deposits not yet recognized as being interglacial, so that Gams' statement seems unfounded. In the second place, two of the most experienced bryologists in this country have named new Quaternary bryophytes. Dr. Grout, an authority on the family Brachytheciaceae, has named a new species of Camptothecium from Aftonian material, and R. S. Williams, also a widely recognized bryologist, has described not only two new species, but also a new genus from Pleistocene material, and all of them in the Amblystegiaceae. It is remarkable that so small a number of North American collections should contain so many interesting species, when many more years of careful and intensive study of European subfossil bryophytes have brought to light a smaller number of new types, which are not even generally accepted. This conspicuous discrepancy between the moss floras of the earliest known interglacial stages of the two hemispheres is difficult to understand, and is of considerable significance.

It is probable that, just as with the phanerogams, whole groups which existed in Tertiary times, but which are now nearly or com-

pletely extinct, persisted into the early part of the Pleistocene. There has been sufficient time for many changes to have taken place since the beginning of Pleistocene times, which was, according to one of the most recent calculations (Leverett, 1932), at least a million years ago. Baker (1920) says: "It is believed that upwards of a million years have elapsed since the first great field of ice covered the country, a period of sufficient length to permit great changes in the species of plants and animals inhabiting the region." This is well shown by the tremendous differences which have occurred in the mammal fauna since early in the Pleistocene. During this time more than ninety-five per cent of the species of mammals have become extinct. Nevertheless, the gastropods, or at least their shells, have not been modified appreciably during the same time, which is accounted for by the fact that a shell is an exceedingly conservative structure whose evolution throughout geological history has been very slow. In the amount of change which they have undergone the mosses occupy a place intermediate between the very plastic mammal group and the nearly static gastropod group. The history of the phanerogamic plants, especially in North America, is so imperfectly known that very little can be said concerning the changes which they have undergone, except that their representation in Tertiary times was, both specifically and geographically, considerably different from the situation now.

TAXONOMIC DISCUSSION OF THE MOSSES

Most of the fossil mosses studied here have been identified with the help of various descriptive manuals designed for present-day species, especially Grout's *Moss Flora* (1928–40), and through comparison with modern specimens. In order to facilitate the comparison with such a large bulk of material, permanent slides were made of a series of the modern species most closely related to the fossils.

The Sphagna occurred as small tangled mats of branches and stem fragments; very rarely as complete leafy stems. They could usually be easily distinguished from the other mosses macroscopically because of their grayish appearance, even when wet, instead of the reddish-brown color of the other mosses. Since the stems and leaves were flattened and extremely fragile, it was impossible, in the usual manner, to make the sections of leaf and stem necessary for exact specific determination. It was in general possible, therefore, to

recognize only the group to which the species belongs, or the "large" species. A detailed investigation of this material by means of regular histological methods would undoubtedly make possible the identification of many more species. It would be necessary, however, to section material embedded in paraffin or celloidin.

List of Species

SPHAGNACEAE

Sphagnum squarrosum Crome. — Branches of this species were easily recognized by the large, squarrose branch leaves.

Present distribution. — Greenland, Labrador, Alaska, Canada, south to the northern United States.

Sphagnum acutifolium Ehrh. (*sensu lato*).

Sphagnum cymbifolium Crome (*sensu lato*). — These long-recognized "species," as understood by the earlier bryologists, are now believed to consist, in reality, of whole groups of species, most of which have a decidedly northern range.

FISSIDENTACEAE

Fissidens sp. — Only one specimen belonging without question to this characteristic genus was found (Pl. I, Fig. 1). The plants are badly damaged, but show the typical sheathing leaves, which are unbordered (Pl. I, Fig. 2) and have cells 10–12 μ in diameter. The specimen is somewhat small to agree well with any of the modern boreal American species having these same characteristics. Nevertheless, I suspect that it is some form of the variable *Fissidens osmundioides* Hedw., which is widely distributed through the northern United States and Canada.

DICRANACEAE

Dicranum Bergeri Bland. — The specimen so named has the upper leaf cells nearly as broad as long, the costa not reaching the leaf apex (Pl. I, Figs. 3–4), and bears only a few serrations on the dorsal side of the leaf at the apex (Pl. I, Fig. 5). It is certainly not in the relationships of the ubiquitous and protean *Dicranum scoparium* Hedw., whose forms have elongated and pitted leaf cells.

Present distribution. — In bogs, Labrador to Alaska; Canada; southward into the northern United States; a boreal to sub-Arctic species.

BARTRAMIACEAE

PHILONOTIS SP. — Only one very small specimen was found, which was recognized by the unbordered leaves and characteristic papillae formed by projecting angles of the wall at the ends of the cells. It does not agree very well with any of the modern species in its plane leaf margins and the rather blunt leaf apex (Pl. II, Figs. 1–3), but any attempt either to propose a new species or to identify an old one from such imperfect material would not repay the trouble. The representation of this genus here is of significance, however, since the species of Philonotis grow in very moist places, or even in water, although never in running water.

AULACOMNIACEAE

AULACOMNIUM PALUSTRE (Web. & Mohr) Schwaegr. — This species was well represented in the collection by many specimens in various states of preservation. Even when the leaf apex (Pl. I, Fig. 6) was lacking the species could be recognized easily by the characteristic thick-walled cells with a central papilla (Pl. I, Fig. 7) and by the tomentose stems. In view of its present common and widespread association with *Aulacomnium turgidum* (Wahlenb.) Schwaegr. in sub-Arctic America, it is surprising not to find it represented in the Aftonian material.

Present distribution. — On the ground in swamps and bogs; North America from the Arctic Archipelago south to Florida in the east and to California in the west.

FONTINALACEAE

FONTINALIS SPP. — Since only small pieces of plants belonging to this genus were found, it was impossible to determine whether or not they originated from the main stem or from the branches. Hence it was considered unwise to attempt to name them, although at least two different species are present in the collection. All modern American species of Fontinalis are aquatic, growing typically in running water, and are characteristic of temperate regions, not reaching even the sub-Arctic zone.

THUIDIACEAE

ANOMODON ATTENUATUS (Hedw.) Hüben. — There is no doubt about this identification, since the areolation, the leaf shape, and the characteristic attenuate branches (Pl. II, Figs. 4–5) agree very well with those of modern material.

Present distribution. — On soil, base of trees, rotten wood, and rocks; very widely distributed in temperate North America.

THUIDIUM DELICATULUM (Hedw.) Mitt. — This identification is beyond question, since the several specimens show the bipinnate and tripinnate branching of the stem, the characteristic papillae of the leaf cells, the paraphyllia, and the stem leaves typical of the species (Pl. V, Figs. 1–2). The most closely related American species is *Thuidium recognitum* (Hedw.) Lindb., which grows in rather dry places.

Present distribution. — On soil, rotten wood, and rocks, usually in moist or wet places; widespread throughout North America east of the Rocky Mountains.

AMBLYSTEGIACEAE

CALLIERGON STRAMINEUM (Brid.) Kindb. — Slender, unbranched plants with leaves imbricated above and spreading below, obtuse and somewhat cucullate at the apex, the costa ending well below the leaf apex, and the alar cells well developed, were placed here. In none of the specimens did I see the radicles produced from the dorsal side of the leaf apex, typical of living material.

Present distribution. — In bogs at high latitudes and high altitudes; Greenland to Alaska, southward to the northernmost United States.

CALLIERGON CORDIFOLIUM (Hedw.) Kindb. — Plants with little-branched stems, spreading leaves with the costa percurrent or nearly so, and the alar cells inflated, but not sharply demarcated from the adjoining cells, were so named. Many of the specimens compared very well with modern material.

Present distribution. — In swamps and bogs; throughout boreal North America, extending southward into the northern United States.

Calliergon Richardsonii (Mitt.) Kindb. — Many forms were found which resembled *Calliergon cordifolium* in many ways, but in which the leaves were shorter and broader, and the costa extended only about half the length of the leaf. Such forms are grouped together here, although there may be at least two species or subspecies represented.

Present distribution. — In bogs and on wet rocks in the mountains; a truly boreal species; Newfoundland, Prince Edward Island, Greenland, Hudson Bay, south to the very northernmost United States.

Calliergon giganteum (Schimp.) Kindb. — The branch leaves of this species are much longer and narrower than the stem leaves, so that isolated branches, which make up the greater part of the material, could have been named only doubtfully if they had not been checked against present-day material. When whole plants occur, however, the pinnate branching, the percurrent costa, and the sharply demarcated auricles of inflated alar cells make the determination certain (Pl. V, Fig. 6).

Present distribution. — In bogs; a distinctly boreal species widespread in northern North America, extending southward to the northern United States.

Calliergon aftonianum, sp. nov. — Plant apparently large, pinnately branched, with the habit of *Calliergon giganteum;* basal leaves oblong, obtuse, 1 mm. long and 0.5 mm. wide (Pl. III, Figs. 1–2); costa very short or even lacking; apical leaves of branch longer and narrower, lanceolate, up to 2 mm. long and 0.3 mm. wide, costa extending about one half the length of the leaf, but never percurrent. Known only from isolated branches. Slide 64 is designated as the type.

This species is closest to *Calliergon giganteum* in its mode of branching and in the similar alar cells, but differs conspicuously and consistently in the longer, narrower, less triangular leaves, which have a much shorter costa.

Calliergon Hansenae, sp. nov. — Stems long, lax, irregularly pinnate, with somewhat attenuate branches; leaves narrowly lanceolate, 1–1.7 mm. long, the average length about 1.5 mm.; costa short, to one half the length of the leaf; apex obtuse to obtusely acute; alar cells very conspicuous. Type, slide 106.

This species is probably most closely allied to the preceding

one or to *Calliergon giganteum*, but is very lax and much resembles some of the forms of Drepanocladus; from this it differs, however, in the peculiar arrangement of the apical leaves, which are mostly obtuse and not at all secund (Pl. III, Figs. 3–4). It approaches Drepanocladus especially in the elongated alar cells (Pl. III, Fig. 5), a feature not ordinarily found in Calliergon; also in the long, narrow leaves and short costa.

Calliergon trifarium (Web. & Mohr) Kindb. — A number of specimens of this species were recognized through their broad, imbricated leaves, which lacked well-defined alar cells and in which the costa was not percurrent. The spirally trifarious leaf arrangement easily seen in living specimens was not obvious in the fossil material, because of the flattening.

Present distribution. — Greenland, across Arctic Canada to Alaska, reaching only the very northernmost United States.

Calliergon turgescens (Schimp.) Kindb. — The abundant specimens of this species were easily recognized from their large size and the very much inflated, turgid appearance of the leafy stems. Under the microscope the leaves show the porose, thick-walled alar cells, the short, thin costa, and the minutely apiculate apex. The curious apiculus is usually missing from older leaves, but may be demonstrated in the terminal leaves, which are not only younger but also better protected from fraying.

Present distribution. — In cold bogs; Greenland, Arctic and sub-Arctic Canada.

Calliergon Kayianum, sp. nov. — Leafy stem relatively large, turgid, 3–5 mm. in diameter, in fragments 0.5 to 2 cm. long, rarely branched, usually bearing at the apex a caducous, budlike structure; leaves widely ovate to nearly orbicular, 2–3 mm. long, 1.5–2.0 mm. wide, averaging 2.5 mm. long and 1.7 mm. wide, but narrowed to the somewhat clasping insertion; apex broadly rounded, not at all acute or apiculate, costa completely lacking (Pl. IV, Figs. 4–7).

This species, which is one of the most common in the collection, and certainly the most conspicuous, much resembles in habit both *Scorpidium scorpioides* and *Calliergon turgescens*. From the former it differs in the symmetrical, not at all secund, leaves, and from the latter, to which it is most closely related, in the nonapiculate leaves with no trace of a costa. An interesting

relationship to *C. turgescens* is shown by the production of extremely easily detached buds at the end of the large main stem. According to Grout (1931), *C. turgescens* has the habit of "reproducing asexually by the falling off of the terminal buds of slender stolons." The big detached buds of *C. Kayianum* make up a great part of the Aftonian material. From the very large variety *gigantea* of *Fontinalis antipyretica* it differs in that the leaves, although concave, are not at all keeled-conduplicate.

Calliergon Kayianum belongs, perhaps, in Williams' new genus Neocalliergon (Williams, 1930a, 1930b), but in view of the great variability, which was apparently characteristic of the complex which we now call Calliergon, during Aftonian and perhaps during later interglacial stages, it is somewhat unsafe to draw too finely the lines between genera. There were apparently whole groups or lines of development which have not persisted into modern times. In the Calliergon material several types apparently represented other unknown species, but were insufficient in quantity or too poorly preserved to be described as new. A study of Calliergon from a much larger collection than this might shed a great deal of light on the origin of the genus and its relation to Drepanocladus. Many specimens were found which possessed characteristics of both Drepanocladus and Calliergon, and appeared intermediate between them. This fact seems to point to a common ancestry for both groups rather than to a parallel development as a reaction to the same environment, as is believed by many bryologists.

Drepanocladus aduncus (Hedw.) Warnst. — Forms with entire leaves and large groups of well-developed alar cells are placed here. Although a great number of forms, including the so-called varieties *Kneiffii* and *polycarpus*, were found, no attempt was made to separate them, because of their infinite variability.

Present distribution. — Widespread almost throughout northern North America; usually in water.

Drepanocladus fluitans (Hedw.) Mönkem. — Forms with serrulate leaves and relatively small areas of alar cells are grouped here.

Present distribution. — Common throughout Canada and the northern United States.

Drepanocladus exannulatus (Gümb.) Warnst. — Specimens with

serrulate leaves, a strong costa, and conspicuous auricles of alar cells are placed here.

Present distribution. — Distinctly boreal; Greenland, Canada, reaching only the northernmost United States.

Drepanocladus revolvens (C. Müll.) Warnst. — This species is characterized mainly by the strongly falcate-secund leaves which have no well-differentiated alar cells. The dark red to nearly black characteristic of living plants persists in the fossil specimens.

Present distribution. — A rather uncommon species of boreal bogs; throughout northern Canada, but reaching only the northernmost United States.

Drepanocladus apiculatus, sp. nov. — Stems rather robust, little branched; leaves 1.5–2.0 mm. long, 0.5–0.7 mm. wide, ovate, tapering to a gradual acumination, at the termination of which is a narrow, often recurved apiculus (Pl. V, Figs. 3–4); very concave, falcate-secund, not plicate; alar cells thick-walled, but otherwise not much differentiated; costa very short, to one half the length of the leaf, rarely more (Pl. V, Fig. 5). Type, slide 183.

This species is apparently most closely related to *Drepanocladus revolvens*, but differs in the peculiarly recurved apiculus and the short costa. So far as I know, no modern species of Drepanocladus has an apiculus on its leaves, although this characteristic still persists in Calliergon.

In the Drepanocladus material there are countless variations and forms which might have been identified, or at least named, most of them under *D. aduncus* and *D. fluitans*. The genus Drepanocladus is still so variable and so plastic, however, that it was considered inadvisable to attempt to segregate varieties and forms from material which grew under conditions which are still not fully understood. As Grout (1931) says of the modern specimens: "Nearly all grow in water or very wet places, and the amount of water and other conditions of their immediate environment appear to modify their growth profoundly. Sometimes two well marked varieties can be found on the same plant."

It appears that, although the genus Calliergon has become somewhat stabilized during the past million years, perhaps by the extinction of intermediate forms, Drepanocladus is still nearly as plastic now as it was during Aftonian times.

Scorpidium scorpioides (Hedw.) Limpr. — This large species, al-

though not common, is represented by several specimens, which are easily recognized by means of their large size and the secund leaves without a costa.

Present distribution. — In swampy and boggy streams and pools; Canada and the northern United States, across the continent.

Amblystegium Juratzkanum Schimp. — Only a single fragment of this small but easily recognized species was recovered. The spreading leaves and the characteristic alar cells are distinctive.

Present distribution. — Widespread through the northern United States and Canada; on rotten wood, moist humus, and stones.

Leptodictyum riparium (Hedw.) Warnst. — The specimens placed here agreed in most respects with modern material, except that some of the leaves are distinctly serrulate, especially toward the base. The apical cells are frequently much shortened, and the remaining cells are shorter than is usual in Drepanocladus, which seems to preclude that genus, a view substantiated by the lack of inflated alar cells. This identification was not considered to be completely beyond question, but the material is too fragmentary to justify the creation of a new species.

Present distribution. — Common throughout the United States and southern Canada.

Campylium stellatum (Hedw.) Lange & C. Jens. — The large leaves with costa short or absent and the numerous quadrate alar cells are well shown in the very large number of specimens present in the Aftonian material (Pl. II, Fig. 6; Pl. IV, Fig. 3). Reasonably long branches occur which have the typical leaf arrangement.

Present distribution. — Throughout Canada, from the Arctic Archipelago south to the northern United States.

Brachytheciaceae

Camptothecium nitens (Hedw.) Schimp. — This species was apparently very common and abundant in Aftonian times, to judge from the quantities of it which are found in fine condition in this material. The plications of the leaves and the abundant tomentum on the stems are extremely well preserved.

Present distribution. — From the Canadian eastern Arctic southward to the northernmost United States.

Camptothecium Woldenii Grout. — Although the type specimen was not seen, several specimens were found which seemed to agree completely with the original description of this species (Grout, 1917).

HYLOCOMIACEAE

Hylocomium splendens (Hedw.) Bry. Eur. — This species is one of the best preserved and most easily recognized in the whole collection. Even the paraphyllia on the stems are still beautifully preserved, and the double costa is conspicuous (Pl. IV, Figs. 1–2).

Present distribution. — Canada and the northern United States; still occurs in Iowa.

POLYTRICHACEAE

Polytrichum strictum Banks. — The identification of this species is facilitated through the tomentose stems and the well-preserved leaves with clearly incurved margins, as well as through the mosses associated with it, since they are bog species. *P. juniperinum*, although very similar, lacks the tomentum on the stem and grows in fields and woods, not ordinarily in bogs.

Present distribution. — Distinctly boreal, growing in Sphagnum bogs and swamps; Greenland, Canada, northern United States.

THE MECHANICS AND CHEMISTRY OF MOSS PRESERVATION

A curious and striking feature of the material just described is the complete and conspicuous lack of certain species, genera, and even whole families of mosses, and of the entire group of hepatics which should certainly be expected on the basis of modern association and distribution of bryophytes. For instance, in our modern boreal bogs there are usually associated with the mosses listed above such genera as Leucobryum, Pellia, Cephalozia, Calypogeia, Lophozia, and Mylia. Since these forms are completely unrepresented in early Pleistocene deposits, it is of course possible to conclude that they were actually lacking during Aftonian times. This conclusion would be almost certainly incorrect, however, because the groups just mentioned are highly developed ones, and, furthermore, to judge by their present wide distribution, must be ancient ones. Since the fossil species occurred in the same associations in which they are still found in nature today and since the hepatics are an old group,

it is reasonable to suppose that the missing species were then present, but for some reason were not preserved. The lack of certain characteristic bog mosses, such as Leucobryum, is so consistent that it appears not to be by accident, but through some idiosyncrasy of the species. The matter of which species are preserved seems to be correlated definitely with the chemical constitution of their cell walls, which in general are much less resistant to hydrolysis than those of higher plants. The cell walls of mosses and hepatics are not made of as permanent and resistant materials as those which compose the cell walls of higher plants, but consist in large part of hemicelluloses, which are usually more easily broken down than true celluloses (Müller, 1905). Hepatics contain even less true cellulose than mosses — only one sixth as much (Lohman, 1903).

According to the long-accepted views of botanists and geologists, peat formation simply amounts to the accumulation of celluloses, hemicelluloses, and their oxidation products. The complete acceptance of this view is reflected by many workers. Weyland (1925) says: "Die schlechte Erhaltung und das Fehlen fossiler Moose überhaupt wird durch die chemische Zusammensetzung der Zellmembranen der Moose erklärt, die zum grössten Teil nicht aus echter Cellulose bestehen und daher leichter zersetzlich sind . . . ."

Rather recently, however, the theory that lignins and their derivatives and, to a much lesser extent, resins and waxes are the materials which persist and accumulate (Fischer and Schrader, 1921) has been gaining ground, especially among chemists. The term "lignin" has been restricted in the past by plant anatomists and morphologists to a somewhat obscure material which is located in secondary thickenings of cell walls and which can be identified by microchemical tests. The same term is used by chemists in a much broader yet specific sense, to cover the aromatic constituents of the cell wall which are characterized upon degradation by the methoxyl group (Fuchs, 1926). This widely conflicting usage and concept is strikingly illustrated by comparing the older chemical analyses of bryophytes by qualitative microchemical methods with more recent analyses on the basis of quantitative tests. None of the early analyses show (Roberts and Haring, 1938) the presence of lignin in bryophytes, whereas the latter demonstrate large amounts of lignins or their derivatives, as determined from the methoxyl content. In fact, more "lignin" is reported for mosses than from some phan-

erogams! For example, Waksman and Stevens (1928), in a study of peat-forming materials, report that "*Hypnum*" contains 21.13 per cent of lignin, whereas "*Sphagnum,*" in the upper, growing, portion and the lower, dead, portion, contains, respectively, 6.97 and 19.15 per cent of lignin. In *Sphagnum cavifolium* and *S. medium* have been reported, respectively, 9.2 and 16.14 per cent of lignin (Stadnikow and Baryschewa, 1930a, 1930b).

Czapek (1899, 1913) reported the occurrence of aromatic constituents, which are now considered to be lignin derivatives, in the cell walls of bryophytes, and found that there is a distinct correlation between the habitat and the type of aromatic compound present. In mosses living in the water or in moist or deeply shaded places he found a material which he named "sphagnol" and which was demonstrated to be strongly toxic to bacteria, fungi, and other organisms. In truly xerophytic mosses, on the other hand, sphagnol is lacking. There occurs a tannin, called "dicranic acid" by Czapek, which is toxic, like sphagnol, but to a lesser extent. In the hepatics, however, there seems to be very little relation between the chemistry of the cell wall and the habitat of the species.

Since peat formation, which is the accumulation of plant residues, probably of an aromatic nature, can take place only under anaërobic conditions (Waksman and Stevens, 1928), the aquatic species obviously stand a much better chance of becoming preserved. In the list given earlier, for example, nearly all the species are either actually aquatic or from very moist habitats. All species which are prevented from being deposited under water, even though they contain the necessary lignins or lignin derivatives, will still not be preserved. As a result, species of the moist but rarely inundated forest floor are found in a fossil or subfossil condition much less often than aquatic species. Progressively, xerophytic mosses such as Grimmia and most species of Rhacomitrium are preserved only under exceptional conditions, and could not be expected to occur in peat at all. For this reason the two most important factors which determine preservation of mosses are their deposition in water and the presence of lignins or related compounds in their cell walls.

Weyland, in his discussion of the poor preservation of mosses in general, has placed significance upon the fact that the moss plant is a gametophyte and thus is ontogenetically different from the ferns and the phanerogams. Although this viewpoint opens some interest-

ing philosophical questions, the moss sporophyte apparently does not have a more resistant cell wall than the gametophyte. This is well illustrated by the almost complete lack of moss sporophytes in known fossil material. It has also been shown that the young sporophyte, at least, contains materials which are easily decomposed (Ziegenspeck, 1926). The true cause of the poor preservation of mosses is undoubtedly that both generations lack the large amounts of resistant vascular and cuticular tissues that are characteristic of the higher groups.

THE CLIMATE OF THE AFTONIAN INTERGLACIAL STAGE

In addition to its purely taxonomic phase, the study of Pleistocene mosses has considerable bearing on the problems of climate and plant distribution during the interglacial intervals. Most mosses are very sensitive to the various environmental factors and, furthermore, usually have a fairly restricted geographical range, as has been pointed out in some detail during the last few years (Steere, 1937a, 1937b, 1938a; Sharp, 1939). Consequently fossil mosses make accurate and convenient indicators of the climatic and ecological conditions under whose influence they grew. Their value in climatic studies of the past has not been sufficiently recognized.

The question of the nature of the climate and life of the interglacial stages is an exceedingly fascinating one, which has had several different and more or less conflicting answers. Savage (1903) says of the plant remains from Dodge Township, Union County, Iowa: "The scarcity in these deposits of fragments of our deciduous forest trees and the presence, in abundance, of leaves and twigs and pieces of wood of cone-bearing trees, such as live at present at higher latitudes, is significant. The absence in these beds of the aquatic moss species that predominate today in the lakes and pools of Iowa, and the occurrence there of species of mosses which now flourish further northward, furnish strong evidence that during the Aftonian age the climate of our state was favorable for the growth of a more boreal vegetation than at present." He continues: "The conclusion seems warranted that many of the plants which are found in the present flora of our state had no place there during the earliest interglacial interval, and that, at our latitude, the climate never became so mild and genial throughout this period as that which the region enjoys during the present age."

Later, Savage (1905), while discussing more Aftonian plants, this time from Oelwein, in Fayette County, Iowa, supports and extends his original opinion, saying: "It is worthy of note that the moss species, whose remains were found in the second member of the section, as well as the pieces of larch wood that came from the horizon of the old Aftonian surface, are forms that thrive at present in more northern latitudes. It is probable that the climatic conditions of the Aftonian interglacial age were, at least toward the close of the interval, less mild and genial in this portion of our country than those which the region has enjoyed in recent times." This view is convincingly supported by the plant materials that have been studied since; in fact, it seems impossible to interpret the evidence otherwise.

Little has been said concerning the vegetation of the Aftonian interval as a whole. Shimek (1910) speaks of "plant-covered land areas similar to those which now prevail in the region," and Baker (1920) considers that "the Aftonian was a time of luxuriant forests."

The Mosses

The modern bryophyte flora of Iowa has been somewhat intensively studied during the last few years, and therefore is rather well known (Bessey, 1884; Savage, 1898; Shimek, 1898, 1907, 1915; Conard, 1912, *et seq.;* Wolden, 1919; Cavanagh, 1921, *et seq.;* Blagg, 1927, *et seq.;* Grout, 1928; Conard and Wolden, 1932; Sayre, 1934).

The great majority of the present Iowan mosses are the same ones that are found in similar habitats throughout Illinois, Indiana, Ohio, and southern Michigan and Wisconsin. Fewer species are reported from Iowa than from any of the states adjacent to it on the east, probably because of the relative scarcity of proper habitats in Iowa and its smaller annual rainfall. As might be expected on the western side of the Mississippi, a slight but perceptible western or southwestern element occurs in the moss flora. The most characteristic indications of such an element are all in the family Funariaceae, namely: *Physcomitrium Hookeri* Hampe, *P. Drummondii* E. G. Britton, *Pyramidula tetragona* (Brid.) Brid., and *Funaria calvescens* Schwaegr.

The relatively small number of species reported from Iowa and the scarcity of unusual species are directly related to the widespread occurrence of only two main types of habitat: prairie, either wet or dry, and occasional open woods. Naturally the mosses are types

characteristic of these habitats, with very few bog or aquatic species represented. In one region of Iowa, and there only, the moss flora departs from this simple formula and is really diversified. This is in the so-called unglaciated area in the extreme northeast corner of the state, where a number of interesting species have been reported (Blagg, 1928a, 1928b; Conard, 1932a, 1932b, 1938). The wonder is not, however, that interesting species have been found there, but that there are so few of them, when one considers the large number of unusual mosses collected by Dr. Holzinger at Winona, Minnesota, not a great deal farther north in the same driftless strip along the Mississippi River. *Bryoxiphium norvegicum*, for example, is almost certain to turn up in northeastern Iowa (Steere, 1937b).

One of the most characteristic features of the present-day Iowa moss flora is the scarcity of aquatic and bog bryophytes. Pammel (1909) says: "There are none of the typical moss bogs found in this state . . . . *Sphagnum* has not been found anywhere in the bogs of northern Iowa." Even though two species of Sphagnum, *S. medium* and *S. cuspidatum*, have recently been reported from Iowa (Cavanagh, 1929a, 1929b), Pammel's last statement still holds true, since they came from wet banks in woods in Muscatine County, which is in the easternmost part of the state and outside the Wisconsin drift area. Thus the bogs are apparently of a nature quite different from those farther north. Beyer (1909), in discussing the peat bogs of Iowa, with special reference to their economic importance, says: "While in high latitudes and high altitudes the club mosses, sphagnums and hypnums contribute very largely toward the accumulation of peat, grasses and sedges are much more important in Iowa peat bogs. Mosses are present occasionally, but play a secondary role." This essential and fundamental difference between the modern bogs of Iowa and the extinct boreal ones is very noteworthy. The boreal type of bog, as exemplified in northern Minnesota, Wisconsin, and Michigan, and from there north into the Arctic, abounds in all types of bryophytes and is probably richer in species than any other type of habitat in the glaciated region, a striking contrast to vegetation in Iowa today.

All the mosses yet reported from Aftonian deposits, together with those discussed in another section of this paper (pp. 82–90), have been species quite characteristic of boreal bogs. This is emphasized by the fact that most of them, including the Sphagna, no longer occur

in Iowa. An examination of their present geographical distribution should demonstrate convincingly that the majority of them are boreal or sub-Arctic species. The most characteristic northern mosses from Aftonian deposits in Iowa are: *Dicranum Bergeri, Calliergon stramineum, C. giganteum, C. cordifolium, C. Richardsonii, C. trifarium, C. turgescens, Drepanocladus exannulatus, D. revolvens, Scorpidium scorpioides,* and *Camptothecium nitens.*

Higher Plants

During the Aftonian interglacial stage nearly the whole state of Iowa must have been covered by a dense coniferous forest of a strictly boreal nature. At least this is the conclusion to be drawn from the fossil material recovered from Aftonian deposits. It is demonstrated by the widespread occurrence of wood fragments, logs, and stumps, as well as leaves, twigs, and cones, in an area where there is no natural forest now. In parts of central and southern Iowa, where there have been no forests within historical times, the old forest bed is so well preserved that fully fifty per cent of the excavations penetrating to its depth reveal it *in situ,* whereas nearly all the rest contain battered logs and sticks (McGee, 1891; Baker, 1920). In some places the water in nearly every well is flavored by products of the slow decomposition going on in the forest layer which is penetrated by the wells. In fact, much of the water in such areas is rendered unfit for drinking because of remains from this forest of approximately a million years ago.

The species of conifers that have been recognized from the débris of the old forests are *Larix laricina* (Macbride, 1896), *Thuja occidentalis* (McGee, 1891), *Picea mariana* (Macbride, 1907), and *P. canadensis* (Macbride, 1907). It is important to notice that these boreal forests, which probably indicate a rather poorly drained region, extended in Aftonian times to the southernmost edge of Iowa and perhaps into Missouri. In fact, the earliest known and best examples of old soils, peats, and forest beds of Aftonian age are found toward the southern edge of the state and, further, the type locality of the horizon is in Union County, which is next to the southernmost tier of counties in the state.

At present, of course, the forest cover of the state is very slight, and much of it is secondary. Even the bogs and swamps are unique in the almost total absence of trees and shrubs. Of the characteristic

inhabitants of boreal bogs during the Aftonian *none* is still found in Iowa. The principal coniferous species of the state now are the highly localized *Abies balsamea*, which grows on cold, wet limestone in the unglaciated northeast corner (Pammel, 1907; Conard, 1938), *Pinus Strobus*, in small and isolated areas; *Juniperus communis*, *J. virginiana*, and *Taxus canadensis*, all of which have a more southern range than the species found in Aftonian deposits. It is rather surprising that the tamarack should be completely lacking in Iowa (Pammel, 1907).

CONCLUSIONS

It is only fair to remark here that there are several criticisms which may be brought to bear on the thesis that the plant remains of the Aftonian deposits present positive evidence that the climate of the interval was boreal.

In the first place, it is evident that topography has a very considerable influence on vegetation, and particularly on the distribution of bogs. The surface of the Kansan drift has been exposed to the elements for an enormous length of time, during which several glacial and interglacial stages have elapsed. As a result, the area in which the Kansan drift is exposed has a well-developed drainage system. The same thing is true of the surface of the Iowan drift and loess, but to a somewhat lesser extent, since they are more recent. It is only within the areas in Iowa which were covered by an ice sheet during the Wisconsin glaciation that one finds a really youthful topography, with its characteristic lack of drainage, which results in numerous lakes and ponds. Even so, bogs are limited to the margins of the Wisconsin drift, where, because of the moraines, the topography is more irregular. Beyer (1909), in his discussion of the distribution of the peat bogs throughout the state, says: ". . . all the peat bogs of commercial importance are confined to the Wisconsin drift sheet. The deepest bogs tested are in those morainal tracts where the surface is most broken. Away from the morainal belt the basins become shallower and the peat thinner, and as a general rule poorer in quality."

Thus it might be said that the lack of boreal mosses and forests may be caused by the lack of suitable habitats. It would be a much more valid argument if the deep bogs in the moraines of Wisconsin drift in the northern part of Iowa had such a flora. But since they

do not and since the typical boreal bogs of northern Minnesota, Wisconsin, and Michigan are also on the surface of the Wisconsin drift sheet, it would appear that climate, or perhaps only some single factor such as temperature or rainfall, is the deciding point, rather than topography. It is probable that earlier in postglacial times boreal species existed in the bogs of Iowa, but have since disappeared as the climate ameliorated with the gradual withdrawal of the Wisconsin ice sheet, which took a good many thousand years (Antevs, 1928). The obsolete, filled-in bogs on the weathered surface of the ancient Kansan drift sheet are an interesting subject for research. Their stratigraphical and biological make-up could be investigated without difficulty by means of borings. Although, strictly speaking, these bogs might be considered postglacial, in a temporal sense they are interglacial, and are so considered by the European glaciologists. Such obsolete interglacial bogs have been carefully studied in Jutland and in northern Germany (Jessen and Milthers, 1928) and the advance and regression of the different floras during two glacial epochs clearly demonstrated. A study of the superficial interglacial bogs of Iowa, with their records of plant and animal inhabitation, might provide some interesting and illuminating data on the question of climates during the different interglacial stages in North America.

In the second place, it might be argued that the boreal bogs of the Aftonian were simply boreal islands in a warm temperate climate, as the isolated tamarack and spruce bogs of southern Wisconsin, Minnesota, and Michigan are frequently considered today. This argument may be refuted in three ways: (1) the genuinely boreal nature of many of the Aftonian species of mosses, which do not now live in the southernmost coniferous bogs; (2) the lack of remains of a really temperate flora, which would certainly have been blown or washed into the bogs, if present; and (3) the enormous areal extent of the Aftonian deposits.

In the third place, the objection might be raised that the boreal species reported from the Aftonian are from the beginning or the end of that epoch, when, as is perfectly obvious, a boreal type of climate must have prevailed, or even an Arctic type in the vicinity of the ice front. The forest beds, with the roots and stumps still in place, which have often been described from the Aftonian deposits, most certainly represent the very end of that interglacial interval,

when the Kansan ice sheet spread its load of débris over the remains of the old forest. In general, however, the plant remains known from the Aftonian so far are to a surprising degree those of distinctly boreal species. Below the forest bed are often other layers of muck and peat which likewise contain traces of plants. Sometimes many feet of exposed fossiliferous strata rest at the bottom on Nebraskan drift and are covered at the top by Kansan till, thus apparently representing a record of a large part of the interglacial period. Yet from such deposits no species of deciduous trees of a true southern nature have been reported. The most temperate type of vegetation was apparently the pine forests; at least, fragments of pine wood have been found in the deeper strata. That traces of more southern types would have persisted, if they had originally been present, is shown by the occurrence of such material in deposits from the second or Yarmouth interglacial interval, after the Kansan glaciation.

In conclusion, it seems to me beyond doubt that the climate of the part of the Aftonian interglacial interval whose deposits have so far been found was much colder and more humid than the present climate of Iowa. Positive evidence of this difference is given by the abundant remains of boreal mosses. To judge from a rough average of the present geographical ranges of the species of plants and animals which have persisted from Aftonian times, the climate of that stage must have approximated the climate which now prevails in the same longitude between five hundred and a thousand miles farther north.

SUMMARY

1. Earlier reports and records of fossil bryophytes, especially those concerned with Pleistocene material, are reviewed.

2. The remarkably fine preservation which has been reported for Aftonian moss specimens is corroborated and illustrated.

3. An annotated list is given of the thirty-three species of mosses (in nearly twenty genera) which have been recognized and named in a large collection of Aftonian material.

4. Four species were so distinct from the most nearly related modern species that they are here proposed as new.

5. Evidence is presented to show that some genera, especially Calliergon and Drepanocladus, were probably more closely related during Aftonian times than they are at present, through a now extinct series of intermediate forms.

6. The absence of many species, which, on the basis of present distribution and association of species, should have been found in this material, is correlated with the chemical composition of the cell walls of the missing species.

7. The great importance of fossil mosses as indicators of the climatic conditions under which they lived is pointed out and their use in climatic studies of the past suggested, since in Pleistocene deposits there are often more species of mosses than of any other group of plants.

8. The temperate and subboreal nature of the modern moss flora of Iowa is contrasted with the boreal and sub-Arctic species of Aftonian times.

9. It is finally concluded that the Aftonian interglacial stage, so far as can be judged by the abundant moss material which has been discovered in its deposits, was much colder and wetter than at present, with a climate like that now existing five hundred to a thousand miles farther north.

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EXPLANATION OF PLATE I

Fig. 1. *Fissidens sp.* The entire fragment, which shows the characteristic distichous leaf arrangement. × 25

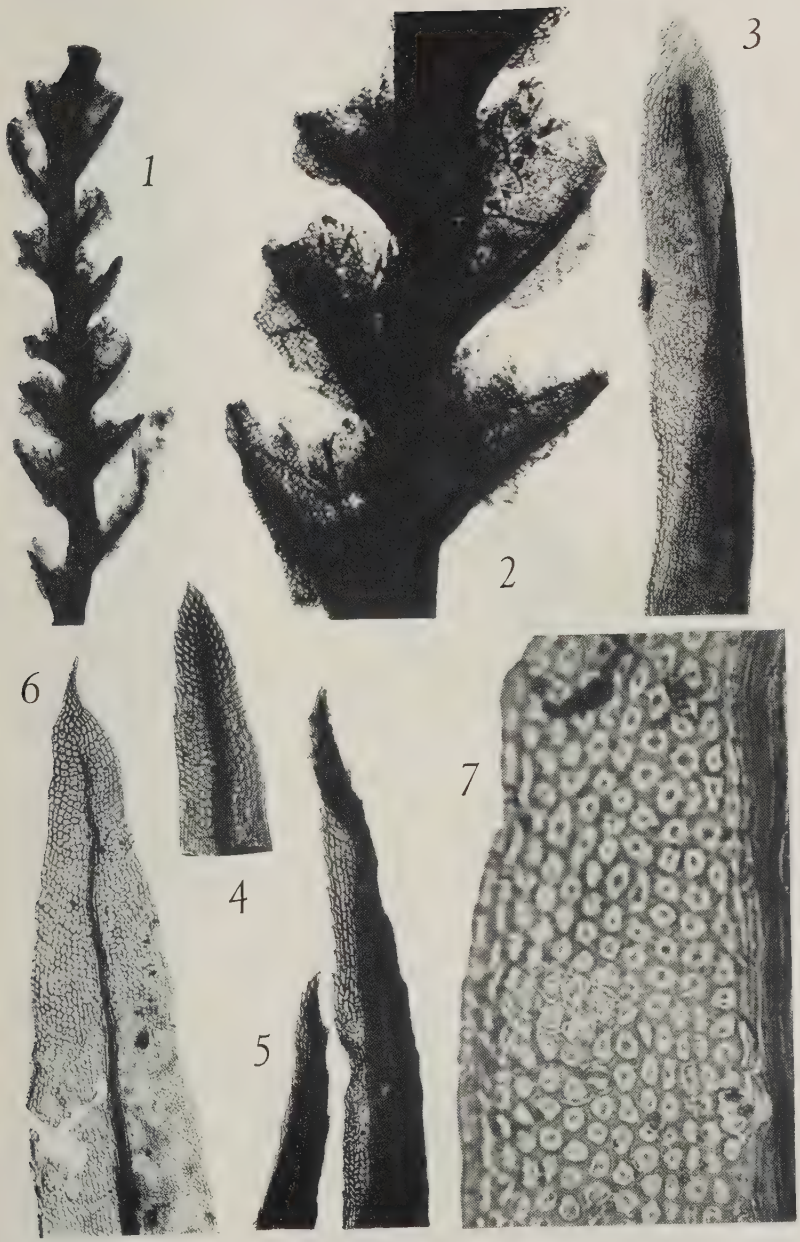
Fig. 2. *F. sp.* Detail of part of stem shown in Figure 1. × 77

Figs. 3–4. *Dicranum Bergeri* Bland. Upper part of two leaves, showing the typical short cells and the costa ending below the apex. × 77

Fig. 5. *D. Bergeri* Bland. Profile view of two leaves. The serration of the dorsal side of the costa is well shown. × 77

Fig. 6. *Aulacomnium palustre* (Web. & Mohr) Schwaegr. Upper part of leaf. × 77

Fig. 7. *A. palustre* (Web. & Mohr) Schwaegr. Detail of same leaf, showing the thick-walled unipapillose cells. × 332



Pleistocene mosses

EXPLANATION OF PLATE II

FIGS. 1–2. *Philonotis sp.* Single leaves. × 77

FIG. 3. *P. sp.* Habit of whole specimen, from which several leaves have been removed. × 20

FIG. 4. *Anomodon attenuatus* (Hedw.) Hüben. Characteristic attenuate branch. × 25

FIG. 5. *Campylium stellatum* (Hedw.) Lange & Jens. A singe typical leaf with conspicuous quadrate alar cells. × 77

FIG. 6. *A. attenuatus* (Hedw.) Hüben. Fragment of main stem, showing more detail of leaf shape than Figure 4. × 25

Pleistocene mosses

EXPLANATION OF PLATE III

FIG. 1. *Calliergon aftonianum*, sp. nov. Single branch leaf. The leaf shape and the short costa are characteristic. × 77

FIG. 2. *C. aftonianum*, sp. nov. Leaves with very short costa from base of a branch. × 60

FIG. 3. *C. Hansenae*, sp. nov. Habit of plant. × 20

FIG. 4. *C. Hansenae*, sp. nov. Apex of plant in Figure 3, showing in greater detail the stem apex, the leaf shape, and the short costa. × 77

FIG. 5. *C. Hansenae*, sp. nov. Basal angle of leaf, showing the elongated, Drepanocladus-like alar cells. × 332

Pleistocene mosses

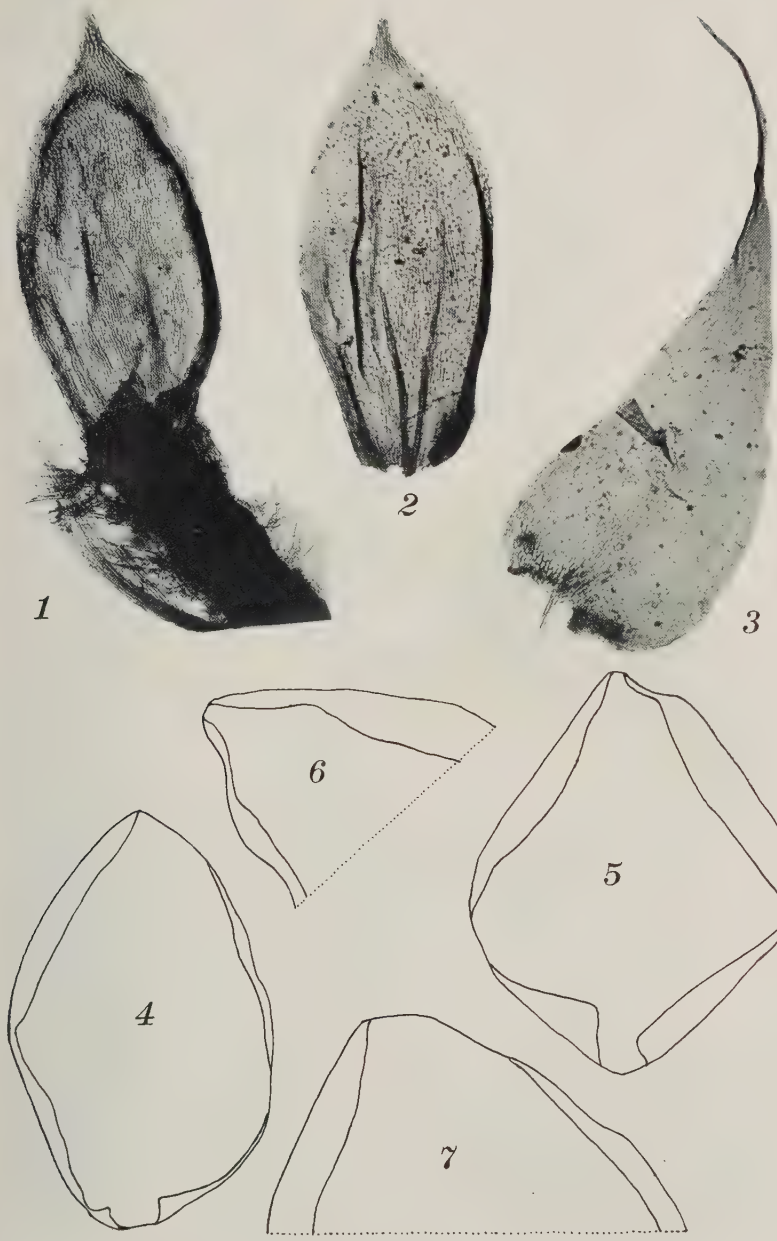
EXPLANATION OF PLATE IV

FIGS. 1–2. *Hylocomium splendens* (Hedw.) Bry. Eur. Leaves, showing the typical double costa and the paraphyllia. × 77

FIG. 3. *Campylium stellatum* (Hedw.) Lange & C. Jens. A single leaf. × 77

FIGS. 4–5. *Calliergon Kayianum*, sp. nov. Whole leaves. × 24

FIGS. 6–7. *C. Kayianum*, sp. nov. Apex of two leaves. × 40



Pleistocene mosses

EXPLANATION OF PLATE V

FIG. 1. *Thuidium delicatulum* (Hedw.) Mitt. Apex of ultimate branch, showing the well-preserved papillae on the leaf cells. × 332

FIG. 2. *T. delicatulum* (Hedw.) Mitt. Habit of branch. × 20

FIGS. 3–4. *Drepanocladus apiculatus*, sp. nov. Characteristic apiculus from two leaves. × 332

FIG. 5. *D. apiculatus*, sp. nov. Whole leaf, showing the costa, the undifferentiated alar cells, the apiculus, and the fungous hyphae. × 77

FIG. 6. *Calliergon giganteum* (Schimp.) Kindb. Alar cells and well-developed costa of branch leaves. × 77

Pleistocene mosses

STUDIES ON CHINESE SPECIES OF GRIFFITHSIA *

CHENG KWEI TSENG

PLANTS of the genus Griffithsia (Ceramiaceae, Rhodophyceae), now credited with a few more than thirty species, are chiefly inhabitants of the warmer seas, although some of them may extend into the temperate zones. As early as 1836 Burnett (Murray and others, 1836, pp. 329, 332) mentioned the occurrence of "*Griffithsia corallina*" (?) in China, without giving the exact locality. The record, like most of the early ones vaguely ascribed to China, is certainly not reliable. In fact, the occurrence of true *G. corallina* (Lightf.) C. Ag. in the Pacific Ocean does not seem very probable, to judge from our present knowledge of its distribution. Since the determination of species of this genus now requires detailed microscopic examination of the reproductive organs, Burnett's record cannot be accepted until the specimen upon which it is based is reëxamined and its identification confirmed. In the regions near the China Sea there have been definitely reported three species [1] from the Malay Archipelago (Weber–van Bosse, 1923) and five [2] from Japan (Okamura, 1930a, 1930b, 1933; Yendo, 1914).

In the past few years the writer has collected fourteen different sets of specimens belonging to this genus. A study of them reveals the presence of five species, one of which has to be proposed as new. All are here added to the floristic list of China for the first time. The species can be distinguished from one another by the following analytic key:

* Papers from the Department of Botany of the University of Michigan, No. 781.

[1] There is also reported a "*Griffithsia sp.*" which resembles, according to its author, *G. opuntioides*.

[2] Yamada (1928) also reported a doubtful record of *G. corallina*. Okamura, in his *Nippon-kaisōsi* (1936; in Japanese), proposed a new species under the name *G. Tome-Yamadai*, described in Japanese only.

A. Cells generally cylindrical to subcylindrical and clavate
  B. Branching scanty, generally lateral, arising from the proximal end, near the basal walls of the cells ..... 1. *G. tenuis*
  B. Branching abundant, apparently dichotomous or subdichotomous, arising from the distal ends of the cells
    C. Frond bushlike, larger, to 10 cm. high; cells generally 4–12 diameters long ..... 2. *G. subcylindrica*
    C. Frond flabellate, smaller, to 4 cm. high; cells generally 2–4 diameters long ..... 3. *G. japonica*
A. Cells barrel-shaped to spherical, at least the upper ones very distinctly constricted
  B. Frond fastigiate, flabellate, branches to 450 μ broad; young branches convergent-furcate ..... 4. *G. rhizophora*
  B. Frond not fastigiate and flabellate, branches to 1,200 μ broad; young branches not convergent-furcate ..... 5. *G. Metcalfii*

1. *Griffithsia tenuis* C. Ag.

(Figure 1)

C. Agardh, Species algarum, II, 1828, p. 131; J. G. Agardh, Epicrisis, 1876, p. 70; De Toni, Sylloge algarum, IV (3), 1903, p. 1284; Collins and Hervey, Algae of Bermuda, 1917, p. 135, pl. 6, figs. 38–39; Børgesen, Marine Algae of the Danish West Indies, II, 1920, p. 462, fig. 423; Okamura, Icones of Japanese Algae, VI (1), 1933, p. 2, pl. 302, figs. 1–6.

Griffithsia thyrsigera Askenasy, Algae, *in* Forschungsreise S. M. S. "Gazelle," 1838, p. 36, pl. 9, figs. 1, 4.

The filamentous frond forms loose tufts to 5 cm. long. It is attached to the substratum by means of vigorous unicellular rhizoids issuing from the decumbent filaments. The branching, which is rather scarce and irregular, is predominantly subsecund. It has already been pointed out by various authors that the branches arise in a very peculiar way; they originate from the proximal ends of the mother cells near the basal walls (Fig. 1) rather than from the distal ends, as in other members of this genus. By this characteristic alone it can readily be distinguished from other species, even those in the sterile condition. The cells are generally cylindrical, sometimes being a little thicker at both ends. They are about 100–180 μ in diameter and 4–6 times as long. Deciduous dichotomous hairs are found around the upper ends of the younger cells. Tetrasporangia are spherical, tetrahedrally divided, and about 80 μ in diameter when mature. No involucral cells accompany them, although there are generally hairs or hair scars below them. Eight to twelve of these sporangia form a ring around the upper ends of the fertile cells, which are 3–4 cells below the tip. Two to three whorls in succession are borne by each filament. Each sporangium occurs on a unicellular

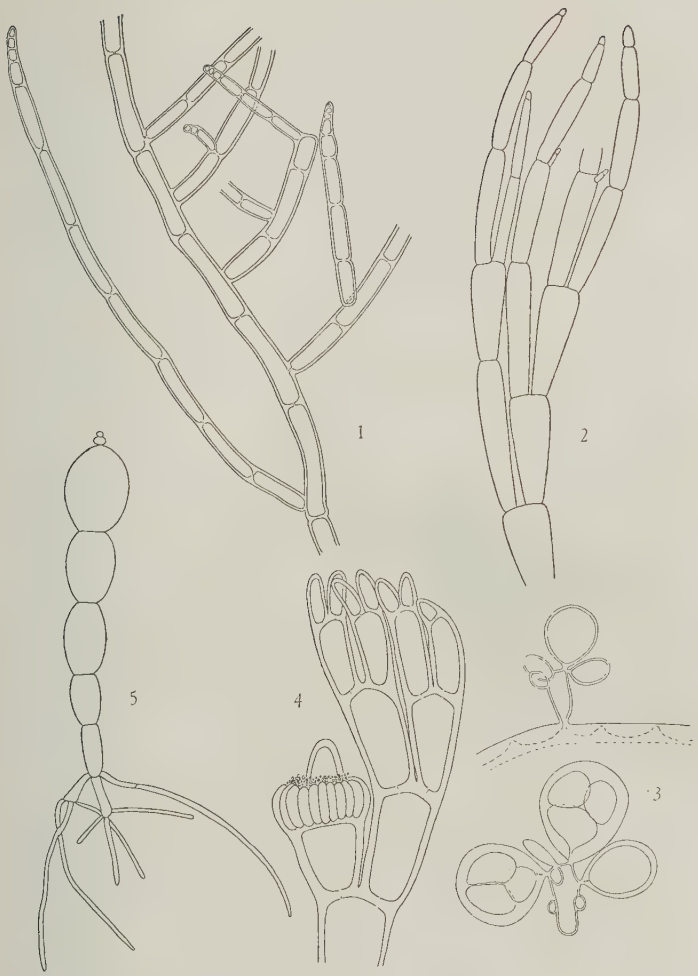


Fig. 1. *Griffithsia tenuis* C. Ag., showing branching. × 16.9

Fig. 2. *Griffithsia subcylindrica* Okam. Upper part of a branch. × 16.9

Fig. 3. *Griffithsia subcylindrica* Okam. Two groups of tetrasporangia. × 211.5

Fig. 4. *Griffithsia japonica* Okam. Upper part of a spermatangial plant, showing branching and spermatangial clusters with involucre. × 25.4

Fig. 5. *Griffithsia Metcalfii* Tseng, sp. nov. A young plant. × 10.6

clavate or pyriform pedicel, 30–40 μ in diameter and 1.5–2.0 diameters long. Neither male nor female plants are found. The plant is dark purplish red, and adheres to paper upon drying.

Habitat.[3] — On sand-covered rocks, at edges of rock pools in the littoral region, Tungshan Island, Fukien, in June (*Tseng 1393*); Hainan Island: Yingkehai, in April-May (*Tseng 971*) and February (*Tseng 2369*), Bakloi, in May (*Tseng 1034*); and West Island, Sama, in January (*Tseng 2351*).

Distribution. — Widely distributed in warmer and tropical seas.

2. *Griffithsia subcylindrica* Okam.

(Figures 2–3)

Okamura, On the Algae from the Island Hatidyo, 1930, p. 99, pl. 8.

Plants of this species form dense caespitose tufts to 10 cm. high. They are attached to the substratum by means of unicellular rhizoids emitted by the basal cells. The branching is subdichotomous and fastigiate-erect with very narrow angles (Fig. 2). The cells are subcylindrical to clavate, about 400 μ in diameter and 4–12 times as long. Tetrasporangia are spherical, being about 80–85 μ in diameter when mature, and are in groups of 3–6, each group with a common pedicel (Fig. 3). These pedicels arise verticillately on the upper ends of fertile cells. The tetrasporangial groups are involucrate with simple short, incurved cells which originate directly from the articulations. Sexual individuals are not found. The plant is brilliantly purplish red when living and firmly adheres to paper on drying.

Habitat. — On rocks in the upper sublittoral region and exposed to strong currents, Yingkehai, Hainan, in February (*Tseng 2379*) and April-May (*Tseng 884, 937*).

Distribution. — Hatidyo, Japan.

3. *Griffithsia japonica* Okam.

(Figure 4)

Okamura, Icones of Japanese Algae, VI (4), 1930, p. 28, pl. 270.

Plants of this species form erect tufts epiphytic on algae and hydroids. They are subdichotomous, fastigiate-erect and flabellate, with the upper branches very closely applied to one another (Fig. 4).

[3] For the different regions on the China coast see Tseng, 1936, pl. VI.

Attached to the substratum by basal rhizoids, they sometimes also develop lateral rhizoids, which issue from the upper parts of the frond. The cells are subcylindrical below and subcylindrical to strongly clavate above. They reach a maximum diameter of 520 μ in the broadened upper portions of the cells; generally, however, they are 300–400 μ in diameter and 2–3 times as long above and 3–4 times as long below. Only spermatangial plants have been collected at Amoy. Spermatangia are densely clustered in whorls around the upper ends of the fertile cells, generally the subterminal ones. They are surrounded by an involucre composed of sixteen or more incurved subcylindrical cells, about 100 μ in diameter and 2–3 times as long (Fig. 4). The terminal cell above the spermatangia often drops off, and the spermatangial clusters seemingly terminate the branchlets. The plant is purplish red and adheres firmly to paper on drying.

Habitat. — On algae and hydroids in the lower littoral region, Kukwang, Quimoy, Amoy, in August (*Tseng 2063*).

Distribution. — Kyushu to Matsushima, Japan.

Although the writer has only the spermatangial plant on hand, he does not hesitate to refer his plant to the Japanese species. According to Okamura, the author of the species, it is so closely related to the European *G. Schousboei* Mont. that he himself is very uncertain whether or not it is distinct from that species, and it seems that Okamura (*loc. cit.*, p. 29) proposed the species on a distributional basis rather than on morphological characteristics: "Considering, on the one hand, that the present plant is in far remote waters from the type locality, and on the other, that I could not find any paper reporting the occurrence of *G. Schousboei* or its variety in the Pacific Ocean, as far as I am aware, I think better to take the present plant as a distinct species. If not a new species, a variety?"

If this is the actual reason, no one would be justified in describing the plant in question as new! Fortunately, *G. japonica* Okam. appears to be a very characteristic plant, at least according to the writer's interpretation of it. It is distinct enough from *G. Schousboei* Mont., which is thicker (to 1 mm. in diameter), nonflabellate, with broader angles in the upper dichotomies, and has its upper cells typically oval to globular, like *G. corallinoides* (L.) Batt. (= *G. corallina* (Lightf.) C. Ag.). The development of tetrasporangial involucral cells on normal branches in some plants of the present spe-

cies seems not to be met with in the European species; Okamura has brought out this difference also. The writer is thus inclined to interpret the present species as rather remotely related to *G. Schousboei* Mont. On the other hand, it seems to be far more closely related to *G. opuntioides* J. Ag., which, however, has cells much longer (4–6 diameters long), somewhat smaller and less clavate, and branches not so closely applied to one another.

Okamura, *loc. cit.*, quoted Yendo's record (1914, p. 277) of *G. Schousboei* Mont. as referring to the present species. Since Okamura may have an entirely different conception of *G. Schousboei* and since the writer has not seen the plant on which Yendo based his report of *G. Schousboei*, the authentic specimen of which he claims to have seen, Okamura's interpretation of Yendo's record will not be followed for the time being.

4. *Griffithsia rhizophora* Weber-van Bosse

Weber-van Bosse, Liste des algues du Siboga, III, 1923, p. 313.

This species has a tufted frond to 2.5 cm. high, which is subdichotomous, fastigiate, and flabellate. The branching is quite profuse; young branches are characteristically furcate and convergent, like members of the genus Ceramium. Cells reach a maximum diameter of 450 μ. They are subspherical to ellipsoidal, 1–2 diameters long above and cylindrical, elongated 2–5 diameters farther down. The few specimens collected are all sterile.

Habitat. — In rock pool at lower littoral region, Yingkehai, Hainan, in February (*Tseng 2410*).

Distribution. — Ceylon; Malay Archipelago.

The vegetative condition of this plant resembles so much the alga from Malay and Ceylon, as described in detail by Weber-van Bosse, that the writer feels justified in classifying it here. He was at first inclined to treat it as a sterile environmental form of the next species, which is described as new. Since these plants were collected in similar habitats, at the same time, and in the same locality, the environmental factors cannot account for the differences. The writer has also found *G. Metcalfii*, sp. nov., in various stages of development, but has seen nothing similar to this. Moreover, the profuseness and the regularity of the subdichotomous, fastigiate, flabellate branches of this species do not occur in the new species.

The plants collected are sterile, however, and the writer has not been able to study authentic specimens of the Ceylon-Malayan plant.[4] Consequently the determination must be tentative.

5. Griffithsia Metcalfii,[5] sp. nov.

(Figures 5–9)

Frons parva, caespitosa, ca. 2.5 cm. alta, bene moniliformis, ramosa irregulariter in lateribus vel subdichotome, cellulis sphaericis vel subsphaericis vel ellipsoidalibus in parte superiore majoreque, ad 1.2 mm. latis, 1.0–1.5-plo longis, in parte inferiore ad basim frondum vel ramorum saepe subcylindricis, multo angustioribus sed longioribus, ad 400 μ latis, 1.5–3.0-plo longis; penicilli numerosi ad apicem cellularum superiorum; sporangia sphaerica, tetrahedraliter divisa, ca. 80 μ lata, circa apicem cellularum fertilium verticillata, solitaria vel 2–3-aggregata in pedicellis brevibus, cellulis involucralibus 1–2 incurvis praedita, ca. 80 μ latis, vulgo 3-plo longis; spermatangia ad apicem cellularum fertilium aggregata, haud terminalia, plerumque 2–5 cellis ab apice remota, nuda, sine involucro; cystocarpia lateralia ad apicem cellarum fertilium, protecta 5–6 cellulis incurvis involucralibus, ca. 100–200 μ latis, 3–4-plo longis; carposporae pyriformes ca. 30 μ latae, 40 μ longa.

Specimen typicum: Yingkehai, Hainan, May 1, 1934, *Tseng 938*, in herb. C. K. Tseng.

This plant forms small tufts to 2.5 cm. high. The frond as a whole is very strongly moniliform throughout (Figs. 5, 9). It is rather irregularly and sparingly branched, the branching being lateral or subdichotomous. The attachment to the substratum is generally effected by means of basal rhizoidal filaments (Fig. 5). Lateral rhizoids usually issue from the decumbent cells, helping with the anchorage. Branches of the same frond sometimes attach to each other by means of short unicellular tenacular cells, and the frond

[4] Ferguson's Ceylon Algae No. 316, on which *G. rhizophora* Weber-van Bosse was based, as well as Mme Weber's Siboga specimens of this species, are not available in this country. Search for it has been made in vain in the herbaria of the New York Botanical Garden and the University of California and in the Farlow Herbarium, which are well known for the richness of their algal collections.

[5] This species is named after Professor F. P. Metcalf, curator of the herbarium of Lingnan University, Canton, China, by whose help the writer was enabled to carry out his first and second trips (in 1933 and 1934) to the floristically interesting island of Hainan, where this and many other new and rare plants were collected.

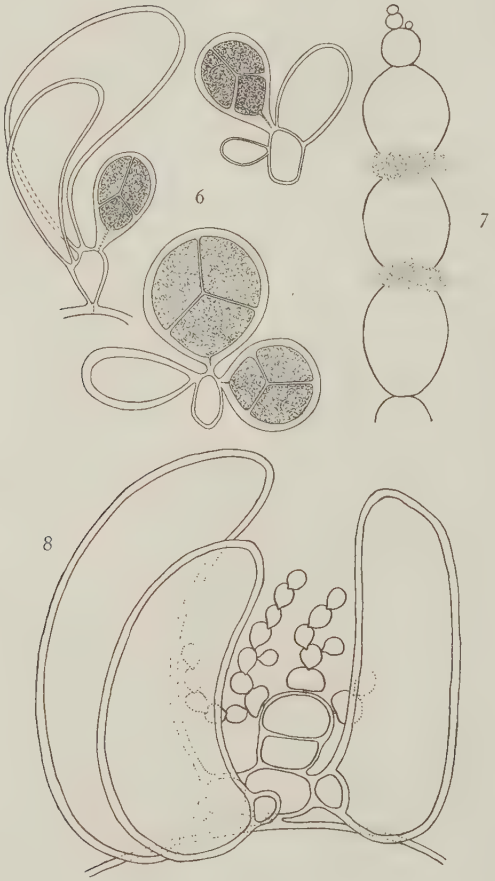


Fig. 6. *Griffithsia Metcalfii* Tseng, sp. nov. Three groups of tetrasporangia, showing different stages of development of sporangia and involucral cells. × 219

Fig. 7. *Griffithsia Metcalfii* Tseng, sp. nov. Upper part of a spermatangial branch, showing spermatangial clusters. × 17.5

Fig. 8. *Griffithsia Metcalfii* Tseng, sp. nov. A young cystocarp. × 127

thus becomes more or less inextricably interwoven below. In the major part of the frond the cells are spherical to subspherical, sometimes ellipsoidal; subcylindrical cells are found only at the very base of the branches of the frond. The beadlike cells reach a maximum diameter of 1.2 mm., and are usually 1.0–1.5 times as long; the subcylindrical ones are much thinner and longer, as a rule about 400 μ in diameter and 1.5 3.0 times as long. The cells are generally

FIG. 9. *Griffithsia Metcalfii* Tseng, sp. nov. Type specimen. × 2.8

largest in the middle portion of the frond or somewhat higher, and attenuate toward both apex and base. The cell wall is rather heavy, reaching 30 μ in thickness. Both young and mature hair clusters are common around the shoulders of the upper cells; they are di- to polychotomously branched, like those of other members of this genus. Tetrasporangia are spherical, tetrahedrally divided, to 80 μ in diameter. Numerous sporangia form rings around the upper ends of the fertile cells. They occur either singly or in twos or threes on short pyriform to subcylindrical pedicels growing out from the

fertile cells. Besides the sporangia, each pedicel also gives rise to one or sometimes two incurved, club-shaped involucral cells, about 80 μ in diameter and generally three times as long, which subtend the sporangia within (Fig. 6). Spermatangial clusters are not terminal. They are found around the upper ends of the fertile cells, which are generally the second to the fifth cells below the apical cell. They are naked, without involucre (Fig. 7). Cystocarps occur laterally at the upper ends of fertile cells, each protected by 5–6 incurved involucral cells (Fig. 8). These are different from the sporangial involucral cells in shape and size, and are much larger below but smaller upward, being about 100–200 μ in diameter and 3–4 times as long. In the development of the fertilized carpogonial branch the supporting cell cuts off another, forming the auxiliary cell, as in the case of *G. corallina* investigated by Kylin. Carpospores when mature are subspherical to pear-shaped and are about 30 μ broad and 40 μ long. This plant is rather soft and is light purplish red; it adheres firmly to paper on drying.

Habitat. — On sand-covered rocks in rock pools in the littoral region, Hainan: Yingkehai, in May (*Tseng 938*, TYPE) and in February (*Tseng 2423*); Pê-ngau-kang, Lohwei, in December (*Tseng 1890*).

The present species resembles the Japanese species *G. coacta* Okamura (1930a, p. 99, pl. 9) so closely that the writer was first tempted to identify these specimens with it. A strong similarity is found in the emission of lateral root fibers from lower articulations and the occasional presence of tenacula between some filaments of the same frond. A more careful study of this species, however, reveals some differences, the most important of which is the presence of involucral cells which are absent in the Japanese plant, as may be clearly seen in the illustrations and description of that species by its author (Okamura, *loc. cit.*, pl. 9, f. 9). The absence of involucral cells in the Japanese species is emphasized and used as the characteristic differentiating it from other species, in the key to the Japanese species of Griffithsia in Okamura's manual of Japanese algae (*Nippon-kaisōsi*, 1936; in Japanese). The spermatangia as well as the cystocarps are not described for the Japanese plant and hence comparison of these structures is not possible. So far as the described vegetative characteristics are concerned, the Chinese plant seems much more strongly and regularly moniliform and much greater in diameter than the Japanese one. Moreover, the present

species is certainly not "dichotomo-fastigiate in upper branches," though that is characteristic of the Japanese plant.

Another closely related species is *G. rhizophora* Weber–van Bosse, which has also been found in Chinese waters (see p. 110). As already indicated in the key and stated in the discussion of that species, the characteristic difference is that the Ceylon-Malayan plant is fastigiate-flabellate, with young branches typically convergent-furcate, whereas the Chinese plant is definitely not so (see Fig. 9). *G. globulifera* Harv. of Atlantic North America and *G. corallinoides* (L.) Batt. of Atlantic Europe are also closely related to the present species. They are, however, much more elegant species, with regularly and profusely dichotomous fastigiate branches and generally longer articulations. Further, *G. globulifera* Harv. differs in its capitate spermatangial clusters and the involucral cells of the tetrasporangial ring, which arise directly from the fertile branch cells, but in the present species the spermatangial clusters are not terminal, and the involucral cells originate from the pedicels, which also give rise to the sporangia.

f. subsecunda, f. nov.

Rami conspicue subsecundi. Specimen typicum: Seven Stones, Pê-ngau-kang, Hainan, April 26, 1937, *Tseng 2504*, in herb. C. K. Tseng.

This form differs from the typical species just described in having predominantly subsecund branching, a more elongated frond, to 6 cm. long, and somewhat smaller, but generally longer cells, which are usually more ellipsoidal than spherical. Rhizoidal filaments are also much more frequently met with; they issue unilaterally like the branches. Plants of this form grow more or less prostrate on sand-covered rocks, whereas those of the typical species grow erect in rock pools; this may account for the vegetative differences found.

Habitat. — On sand-covered rocks in the littoral region, Seven Stones, Pê-ngau-kang, Hainan, in April (*Tseng 2504*, TYPE).

SUMMARY

To date no Griffithsia has been definitely reported from the China coast, although there is a doubtful record of *G. corallina* by Burnett. Five species are identified in the writer's collections of this group of plants. All these materials come from the South China

coast — from Amoy, Fukien, down to the island of Hainan, Kwangtung. One species, *G. Metcalfii*, is here described as new; it belongs to the *G. corallinoides* (= *G. corallina*) group. A new form, f. *subsecunda*, of this new species, is also described. Of the remaining four species one (*G. tenuis* C. Ag.) is widely distributed in warmer waters; another (*G. rhizophora* Weber–van B.) was formerly known to occur only in Ceylon and the Malay Archipelago; the remaining two (*G. japonica* Okam. and *G. subcylindrica* Okam.) have hitherto been known only from the southern part of Japan.

The writer wishes to express his thanks to Dr. Wm. Randolph Taylor, professor of botany, the University of Michigan, under whose direction the present study has been carried on.

University of Michigan

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CYTOLOGICAL STUDIES ON *SPIRONEMA FRAGRANS* LINDL. AND CERTAIN OTHER COMMELINACEAE

SU-HSUEN WU

Introduction

SPIRALIZATION and the behavior of chromosomes in Tradescantia have been studied in considerable detail by many cytologists (see Kuwada, 1932, 1938; Nebel, 1932a, 1932b, 1933, 1935; Kuwada and Nakamura, 1933, 1934a, 1934b, 1935; Sax and Humphrey, 1934; Nebel and Ruttle, 1935, 1936a, 1936b). Spironema and others of the Commelinaceae, however, seem to have been somewhat neglected, nor has the nucleolus of the Commelinaceae been much discussed. The present study deals fully with the structure and behavior of the mitotic and meiotic chromosomes of *Spironema fragrans* Lindl., reports the origin and the development of the nucleolus, and analyzes the relationship between the chromosomes and the nucleolus.

This study, undertaken in the Department of Botany, University of Michigan, was conducted under the direction of Professor Wm. Randolph Taylor, to whom the writer is greatly indebted for valuable suggestions and helpful criticism. She also wishes to express her appreciation to Dr. J. T. Baldwin, Jr., for assisting in revision of the manuscript.

Materials and Methods

Spironema fragrans Lindl. was chosen for detailed analysis because of its large chromosomes and its many rapidly growing roots. *Neodonnellia grandiflora* Rose and *Rhoeo discolor* Hance served only as supplementary material. *R. discolor* has two forms: one with leaves which are dark purple beneath and the other with leaves green on both sides. The latter was the form investigated.

For studying the chromosome number and morphology the permanent root-tip smear method of Warmke (1935), the modified

root-tip smear method of Brown (1937), and the modification of LaCour's root-tip smear method for the Feulgen "nuclear reaction" by Mensinkai (1939a) were tried. All yielded satisfactory results, but the last two were superior, for they gave sharper differentiation of the chromatic elements. Because of difficulty in obtaining many polar views of metaphase plates in smears, the present study is almost exclusively based on preparations made by the paraffin method; smears were used only for selecting material.

It was not easy to secure adequate fixation, especially for the chromosomes between late prophase and anaphase. A number of fluids were employed: Bouin's, LaCour's 2BE mixture, Navashin's, Flemming's strong solution, Hermann's, and Taylor's modification of Flemming's fluid. In general the last three gave the best results. Addition of maltose or urea produced little improvement. The writer modified the Flemming type of fixative by mixing equal parts of 1 per cent chromic acid and glacial acetic acid, to 5 c.c. of which were added 2 c.c. of 2 per cent osmic acid in 1 per cent chromic acid. The spiral nature of the chromosomes was exhibited after two hours' fixation with this fluid. None of the fluids mentioned, however, revealed clearly the internal structure of mitotic chromosomes at metaphase and anaphase. Pretreatment by exposure of root tips to vapors of concentrated HCl or HNO_3 was advantageous for showing this internal structure. Proper duration of exposure was determined by experiment. With HCl, exposures producing equally good results varied from 30 seconds to 2 minutes; after an exposure of 5 minutes no clear figures could be found. HNO_3 required 15 minutes. The root tips were washed in distilled water for 30 minutes after the exposure, then fixed with one of the fluids mentioned above. Fixation was followed by washing and dehydrating; embedding in paraffin was done in the usual fashion.

Sections were cut from 5 to 12 μ in thickness and stained with iron-alum-hematoxylin. Newton's gentian-violet method and Smith's modification of this technique gave good results, too, but neither was found to be as practical as hematoxylin. The Feulgen stain, prepared after Coleman (1938), who used Norit as a decolorizing agent, was also employed. Sections treated in this way afforded excellent differentiation of chromosomes against a colorless background. The solution showed no change even after three months. Light Green was occasionally used as a counterstain.

For the study of meiotic chromosomes the smear method of Taylor (1924), in conjunction with the fixing fluids mentioned above, was employed exclusively. It proved to be the most satisfactory, although the author's modification of Flemming's method was better for demonstrating the doubly coiled nature of the chromosomes.

Observations

I. somatic divisions

A. *Number and Morphology of the Chromosomes*

1. *Spironema fragrans* Lindl. — Darlington (1929), in a study of Tradescantia, described the chromosome morphology of *Spironema fragrans* as: two pairs of long chromosomes each with a submedian constriction, one pair with two submedian constrictions, and three pairs with subterminal constrictions, the shortest pair having satellites. Anderson and Sax (1936) reported in microspore nuclei of this species two chromosomes with median or submedian constrictions and four with subterminal constrictions. In the present material there are six pairs of chromosomes in root tips. Chromosomes *aa*, *bb*, and c_1c_2 are large, with submedian constrictions. No satellites or secondary constrictions were observed (Pl. I, Figs. 1–5). The *a* and *b* pairs correspond to the two pairs of long chromosomes in Darlington's description. The *c* pair are heteromorphic and correspond to Darlington's third pair of chromosomes, but here no secondary constrictions were observed. One of the *c* pair of chromosomes, c_1, has a constriction about one third of the way from one end (Pl. I, Figs. 1–4). This chromosome is more or less ring-shaped at metaphase. At anaphase its two arms straighten out, but the longer arm still bends slightly inward (Pl. I, Fig. 4). The c_2 chromosome is smaller than c_1 and has a submedian attachment. Its two arms are parallel to each other at early metaphase (Pl. I, Fig. 3) and form a V-shaped chromosome at anaphase, with one arm slightly shorter than the other (Pl. I, Fig. 4).

Richardson (1934) reported that in one slide of *Spironema fragrans* an extra fragment was found to lie sometimes very close to one of the submedian bivalents. Darlington (1929), Koller (1932), and Whitaker (1936) have observed fragments and unequal pairs of chromosomes in Tradescantia. Darlington attributed the inequality of these chromosomes to a loss through fragmentation. In the

present material there is no direct evidence for fragmentation except in one instance: in a preparation pretreated with HCl chromosome c_1 shows a secondary constriction in its longer arm (Pl. V, Fig. 33a). If dimorphism of the *c* pair of chromosomes was caused by a fragmentation in chromosome c_2, this fragmentation might be expected to have occurred in the region of the secondary constriction. Such a secondary constriction was not observed in ordinary preparations, however. The abnormality may represent a hybrid character.

The *dd*, *ee*, and *ff* pairs are short chromosomes with closely subterminal constrictions (Pl. I, Figs. 1–4). It is difficult to distinguish among them by size or morphology. Careful study shows that one *d* chromosome bears a single satellite at the distal end of the short arm, but this SAT chromosome is not much shorter than the other subterminal chromosome, as was true of the SAT chromosome described by Darlington. The other *d* chromosome has two satellites in tandem. The distal satellite is usually larger than the proximal one (Pl. I, Figs. 1, 6, 8); occasionally they are equal in size (Pl. I, Fig. 7) or the proximal one is larger than the distal (Pl. I, Fig. 9). If the interpretation of Mensinkai (1939b), that the SAT filament is a continuation of the chromonema and that the satellite is a spiralized end of the chromonema, is valid, it can be applied to explain the difference in size of the tandem satellites as due to the fact that the gyres contract differently in fixation. At anaphase, however, the two daughter chromosomes of the tandem SAT chromosome often show the same difference in number of satellites as the *d* pair of chromosomes at metaphase (Pl. I, Figs. 8–9), i.e. one daughter chromosome bears one satellite and the other two, in tandem. This suggests that one of the satellites may not have split. The dissimilarity of the two members of the *d* pair of chromosomes seems to be another piece of evidence for the hybrid nature of the strain of *Spironema fragrans* used in the present work. Chromosomes heteromorphic with respect to the presence or the absence of the satellites or in regard to their size have also been observed in Galanthus (Satô, 1937b), in Lobelia (Okuno, 1937), in Allium and Trillium (Mensinkai, 1939a), and in Crocus (Pathak, 1940).

2. *Neodonnellia grandiflora* Rose. — This plant appears not to have been previously investigated. The chromosomes are comparatively small and numerous in the root tips: 2n = 32 (Pl. III, Figs. 14–15). Two pairs are slightly submedian in attachment, and the

rest are all subterminal and arbitrarily divisible into three classes according to size: three pairs of larger chromosomes, two pairs having terminal satellites on the short arms and the satellites of one pair being smaller than those of the other (Pl. II, Figs. 10–11); five pairs of medium-sized chromosomes, without satellites; and six pairs of small chromosomes, one pair with terminal satellites on the short arms. There are, however, no sharp distinctions between the successive classes. The gradation in size from the largest to the smallest chromosomes is apparent in Plate II, Figures 10–11.

3. *Rhoeo discolor* Hance. — According to Darlington (1929), in the somatic division of *Rhoeo discolor* there are four chromosomes with the short arm less than half the length of the longer one and eight chromosomes submedian in attachment. Sax (1935), in a study of the meiotic chromosomes of *R. discolor*, stated that six of the twelve chromosomes in the ring are distinctly heterobranchial, but Anderson and Sax (1936) described, in the microspore nuclei, two chromosomes with subterminal fiber-attachment constrictions and four with median ones. In the present material three pairs of the chromosomes have more or less median fiber-attachment constrictions, and the other three pairs have the fiber-attachment region at about one third of the distance from one end, with one pair of this latter group bearing satellites (Pl. II, Figs. 12–13; Pl. III, Fig. 17). Darlington observed that the two SAT chromosomes are dissimilar and that one chromosome has a second constriction, but this is not true of the material at hand. The only dissimilarity observed by the writer is that often one of the medianly constricted chromosomes is somewhat ring-shaped at metaphase; no difference in size or in structure was seen (Pl. III, Fig. 17). The satellites were not clearly observed in anaphase (Pl. III, Fig. 18).

B. *Chromosome Structure and Behavior in Spironema fragrans*

1. *Prophases.* — In early prophase more or less regularly coiled threads evenly distributed throughout the nucleus are observed. In most instances the spirals appear as single coils (Pl. IV, Fig. 22), but occasionally, in the same nucleus, their duality can be seen in certain parts (Pl. IV, Fig. 23). It later becomes clearly evident that the spirals are double; they are in reality the sister chromatids formed at the last premetaphase. Still later the nuclei become much larger; the nucleoli are near the nuclear center instead of being in

the region of the poles, as at telophase; and anastomoses between paired chromatids occur less frequently, if at all. The sister chromatids are oriented as at telophase (Pl. IV, Fig. 24). The matrical material is not evident at this stage, the suggestion being that it contributes to the formation of the nucleoli. The coils of the chromatids now stretch considerably, and the double spirals are more clearly and regularly apparent (Pl. IV, Fig. 25). Next the sister chromatids gradually draw close together (Pl. IV, Fig. 26), this approximation being accompanied by a general contraction of the chromosome. An untwisting and a relaxing of the coils are also noticeable at this stage (Pl. IV, Fig. 27). Contraction with relaxation of the old spirals is caused by new spirals within them, which bring about an internal twist of the chromatid; the new spirals are not visible until late prophase. They may be called "minor spirals," corresponding to the minor spirals observed in meiosis. As contraction continues the chromosomes become thicker, and each chromatid assumes a corrugated appearance, which is the first sign of the minor spirals. Meanwhile the chromatids have untwisted rapidly. One can find (Pl. IV, Fig. 29) a longitudinal splitting throughout each chromatid of one chromosome, while the chromatids of another chromosome exhibit only an untwisting in certain parts. In later stages, seldom in early ones, a differentiation of the chromonemata and the achromatic matrix is seen. The matrical material gradually increases and, when stained, obscures the duality of the chromatids.

2. *Metaphase.* — As the nuclear membrane disappears, the individuality of each chromosome is quite apparent, and the chromosomes become aligned at the equatorial plate, their fiber-attachment regions being toward the center of the plate and their arms in the axis of the spindle. Relaxation of the relic spirals has been completed, but relational coiling can still be observed at early metaphase (Pl. V, Fig. 32). In preparations pretreated with HCl or HNO_3 the duality of the chromatids can be clearly seen. Each consists of two chromonemata; the metaphase chromosomes are quadripartite (Pl. IV, Fig. 30).

Relaxation of relational coils seems caused by the formation of minor spirals. In certain parts of the chromosomes, where minor spirals are observed, there are few relational coils; in other parts, where no minor spirals appear, more relational twists remain (Pl. IV, Fig. 29). This relaxation is completed by the time the minor spirals

reach their full expression. The untwisting and the development of the minor coils proceed from the ends of the chromatids toward the primary constriction, as is clearly shown in Plate IV, Figure 29.

3. *Anaphases.* — Each anaphase chromosome consists of two sister chromatids intertwined (Pl. IV, Fig. 31; Pl. V, Fig. 33). At this stage the satellites and their filaments are single (Pl. V, Fig. 33b). The matrix can be seen clearly at both metaphase and anaphase, but it is usually not uniformly distributed, probably because of variations in the effectiveness of the pretreatment.

4. *Telophases.* — The chromosomes become massed together as they reach the poles. The chromosome structure, though obscured, is the same as at anaphase, as can be seen in the arms of the chromosomes which project from the mass. Soon the chromosomes begin to expand in their distal parts, where they have the form of two intertwined spirals (Pl. V, Fig. 34). At this point, because of their expansion, the individuality of the chromosomes is again apparent, and — in spite of a decrease in stainability — their spiral nature is clearly revealed (Pl. V, Fig. 35). The karyolymph is differentiated at this stage, and a nuclear membrane is formed about each daughter chromosome group. Nucleoli are developed at the proximal ends of certain chromosomes. Anastomoses appear between the chromosomes. One has the impression that when the chromosomes draw apart from each other after being once closely appressed, interconnections remain. In certain parts of the chromosomes there is a single helical spiral; in other parts double spirals are intertwined (Pl. V, Figs. 35, 39). The chromosomes are prominently oriented at telophase (Pl. V, Figs. 36–39), a condition which results from the anaphasic arrangement of fiber-attachment regions toward the poles when the arms of the chromosomes are spreading behind. This disposition of the chromosomes is kept until prophase.

5. *Interphase.* — Interphase is characterized by a so-called "reticular" aspect arising from a further expansion of the telophase chromosomes. As expansion continues the spirals are much loosened and the dyads become extremely thin. At points where anastomoses are drawn out and where two chromatids intertwine thickenings occur, so that the nucleus has a knotted aspect. Later these dyad threads get thicker, and the anastomoses are lost. This increase in thickness is probably accompanied by contraction of the chromosome as a whole, and the contraction brings the sister chromatids so

close together that they give the appearance of being single spirals, as they do at early prophase.

C. *The Nucleolus*

Van Camp (1924) considered that the nucleolus arises in telophase from small granules which flow together. Marshak (1931) described a close relationship between the chromosome matrix and the nucleolus substance. Gates and Pathak (1939) also observed the nucleolus to originate, in Crocus, as small globules, but at a particular region of definite chromosomes. Recent investigators (Nandi, 1937; Satô, 1939; Jacob, 1940; and Pathak, 1940) have reported small granules which are present in early telophase chromosomes and which contribute to the formation of the nucleolus. These workers, in contradiction to van Camp and Marshak, consider that the small granules aggregate in nucleoli-organizing regions of the SAT chromosomes and form a definite number of nucleoli under the influence of these regions, as described by McClintock (1934).

Heitz (1931a) postulated that all plants have satellites or secondary constrictions from which nucleoli arise. The nucleoli are correlated with the satellites in number, size, and position. Heitz (1931b) found, however, in *Vicia faba* and *V. monanthos*, which have only two SAT chromosomes, instances in which a micronucleus, formed from a single lagging chromosome without a satellite, had a nucleolus. This implies that even when the SAT chromosomes are absent nucleoli will arise. Matsuura (1938) observed that, whereas in *Paris hexaphylla* the nucleolar development is related to the SAT chromosomes, in *Trillium kamtschaticum*, where there are neither SAT chromosomes nor secondarily constricted chromosomes, the nucleolus nevertheless originates at given ends of certain chromosomes. He also reported, in an abnormal individual, that each chromosome formed a micronucleus and developed its own nucleolus. Satô (1936a, 1936b, 1937a, 1937b, 1938), basing his opinion on a series of investigations dealing with the relationship of the nucleolus and the SAT chromosome, agreed with Heitz's hypothesis. In 1938 he observed, however, that there are two SAT chromosomes in some species of Leucojum and Sternbergia, but four nucleoli in the same plants. All the evidence mentioned above shows a tendency to revision of the interpretation assigning the origin of the nucleolus to a particular chromosome pair and to a consideration of it as a func-

tion of the chromosomes as a whole. Since all these facts were observed in abnormal individuals, however, most investigators are still in agreement with Heitz's hypothesis.

1. *The relation of nucleolus and chromosomes.* — There is only one pair of SAT chromosomes in *Spironema fragrans*, but as many as three nucleoli are present at telophase (Pl. V, Fig. 38). At prophase and metaphase commonly one, very often two, occasionally three, nucleoli are to be seen (Pl. IV, Figs. 22, 24–27, 29). A striking fact is that, at metaphase, a nucleolus may be attached to a submedianly constricted chromosome without a satellite. Similar attachments were frequently found at later stages (Pl. VI, Fig. 45). The nucleolus is sometimes related to chromosome *a* (Pl. VI, Fig. 45), at other times to other chromosomes: to chromosome *b* (Pl. VI, Fig. 46) or chromosome c_1 or c_2 (Pl. VI, Fig. 47), for example. The nucleolus is not at a definite locus, though it is always attached to the longer arm of metaphasic chromosomes. A relation between the nucleolus and the subterminal chromosomes, including the SAT chromosomes, was observed in different nuclei (Pl. VI, Figs. 48 49). It seems that any chromosome may produce a nucleolus. Often a faintly stained membrane-like structure connects the nucleolus and the chromosomes (Pl. VI, Figs. 45, 47, 49). Though the nucleolus remains large and clear in metaphase, no nucleolar divisions have been found. The nucleolus usually disintegrates in the cytoplasm after detachment from the chromosomes.

2. *The origin and behavior of the nucleolus.* — Nucleoli usually do not appear before the daughter nuclei are well organized (Pl. V, Fig. 35). As telophase advances, a nuclear membrane arises, and the chromosomes become arranged at the periphery of the nucleus with the proximal ends of their arms still oriented at the pole. Soon a nucleolus appears in the midst of the chromosomes (Pl. V, Fig. 36). Its relation to the chromosomes can be seen from a polar view or, at least, from an oblique view (Pl. V, Figs. 36–38). One pair of SAT chromosomes is clearly attached to the nucleolus in the region of the satellites (Pl. V, Fig. 36). All nonsatellited chromosomes in the same nucleus are, however, also attached to the same nucleolus. Two comparatively large nucleoli and two small nucleolus-like granules are connected to the chromosomes with many faintly stained threads (Pl. V, Fig. 37). These two small granules are considered to be a beginning of nucleolar development; they probably fuse with each

other or with other collections of nucleolar material to form a larger nucleolus. There may be three nucleoli in the same nucleus (Pl. V, Fig. 38), and they may be in direct contact with the chromosomes or else connected with them by fine threads. These observations suggest that when the fiber-attachment regions of the chromosomes are regularly arranged and close together one large spherical nucleolus is formed. When they are loosely and irregularly arranged two or three nucleoli may be developed at the same time. Incipient nuclei usually show the same number of nucleoli (Pl. V, Fig. 39). The development of a nucleolus seems caused by the gradual addition of nucleolar material arising from the chromosomes (Pl. V, Fig. 36) or by mutual contact of small collections of nucleolar material (Pl. V, Fig. 37). If the chromosomes remain at the periphery of the nucleus the fully developed nucleoli become detached from them and move into the center of the nucleus. The nucleoli maintain the same position through interphase and early prophase (Pl. IV, Fig. 24).

At middle prophase, when the chromosomes become thicker, they usually surround the nucleolus (or nucleoli), and are so closely associated that it is difficult to detect which parts are in contact with it. This phenomenon is more prominent in *Rhoeo discolor* (Pl. IV, Fig. 28). These observations indicate a strong affinity between the chromosomes and the nucleolus at this stage; possibly there is then a transfer of material from the nucleolus. At later prophase only one or two chromosomes, and these not always the same ones, still remain in contact with the nucleolus. The relation of the nucleolus and the chromosomes at prophase is shown in Plate V, Figures 40–41, and Plate VI, Figures 42–44. Chromosomes with both submedian and subterminal constrictions and both satellited and nonsatellited chromosomes were observed to be attached to the same nucleolus (Pl. VI, Fig. 44), or one homologue was attached to the nucleolus and the other was near by (Pl. VI, Fig. 43, *right*), or two nonhomologous chromosomes were related to the same nucleolus (Pl. VI, Fig. 42, *right*). It is interesting to notice that, whatever the arrangement, the prophasic chromosome is always in contact with the nucleolus by the distal end of its short arm. The satellited chromosomes attach to the nucleolus by their satellites instead of by the SAT filament (Pl. VI, Fig. 43, *left*), as observed by Heitz (1931a) and many other investigators. Comparison of nucleolus–chromosome relationship at prophase with that at metaphase shows a movement

of the nucleolus from the distal ends of the short arms of the chromosomes to the distal ends of the long arms. When the nucleolus migrates from one end of a chromosome to the other, the nucleolar material may be evenly distributed through the whole length of the chromosomes. Apparently the membrane-like connection between the nucleolus and the chromosomes is material passing from the nucleolus to the chromosomes. Most investigators hold the view that the nucleolus remains firmly attached to its locus of organization, or near it, from the time the nucleolus is organized until its disappearance. Seemingly this is not true of the present material.

In *Rhoeo discolor* the origin and the behavior of the nucleolus are essentially the same as in *Spironema fragrans*. Here, too, there is only one pair of SAT chromosomes. The maximum number of nucleoli is four. The attachment of the nucleolus to each type of chromosome has been recognized in different nuclei at prophase. Three chromosomes with almost median constrictions are attached to nucleoli as shown in Plate VI, Figure 50. In the submedianly constricted chromosomes the nucleolus is usually attached at prophase to the distal end of the short arm, but occasionally to the long arm (Pl. VI, Figs. 51–52). At metaphase the nucleolus has been found only a few times (Pl. VII, Fig. 53). Movement of the nucleolus from one end of the chromosome to the other is not shown for this material, but in Plate VII, Figure 53, one can see the nucleolus attached near the middle part of the arm instead of at the end.

II. MEIOTIC CHROMOSOME STRUCTURE AND BEHAVIOR IN *SPIRONEMA FRAGRANS*

A. *First Meiotic Division*

The spiral structure of meiotic chromosomes, observed in 1880 by Baranetzky, has been described in many plants. Kuwada and other Japanese workers, in a series of papers, have described the chromonemata of metaphase chromosomes as "double-coiled." Similar reports have been made by Darlington (1935), for Fritillaria, Sax (1935), for *Rhoeo discolor*, Nebel and Ruttle (1936b), for *Tradescantia reflexa* and *Trillium erectum*, and Naithani (1937), for *Hyacinthus orientalis*. Koshy (1934), Hoare (1934), Huskins and Smith (1935), Huskins (1937), and other workers, however, regard the chromonema at this stage as single-coiled.

1. *Diakinesis.* — In Spironema, though there are not sufficient preparations for studying earlier stages of meiosis, the double-coiled structure is apparently not present in the leptotene chromosome (Pl. VIII, Fig. 68). At diakinesis the chromosomes are so compactly twisted, and usually so deeply stained, that it is difficult to analyze the structure in detail (Pl. VII, Fig. 55). Because of the evidence of later stages the reticular appearance is considered to result from a number of spiraled chromonemata twisted together, and the less-stained substance is thought to be the matrix. The chromatids are mutually parallel, with corresponding gyres arranged at the same level, thus producing a regular reticulum. As the process advances, some of the chromosomes form bivalent rings (Pl. VII, Fig. 54 a–c), and others have the two distal parts parallel (Pl. VII, Fig. 54d). In late diakinesis there are three more or less ring-shaped tetrads and three cross-formed associations (Pl. VII, Fig. 56). The so-called "kinetochores" or "centromeres" are clearly seen in Plate VII, Figure 56, a pair in each dyad. The transition from the stage in Figure 54 to that in Figure 56 must be rapid, for no intermediate forms were observed. The internal structure of the chromatids, at the stage shown in Figure 56, gives the appearance of transverse bands embedded in the matrix. Under certain conditions of distortion this structure — continuous spirals and longitudinal splitting of each of the chromatids — can be observed more clearly (Pl. VIII, Fig. 62).

2. *Metaphase.* — Some of the chromosomes begin anaphasic movement before the others (Pl. VII, Fig. 57), and it is difficult to find a complete chromosome set of three rings and three crosses at full metaphase. However, three ring-shaped chromosomes from one cell (Pl. VIII, Fig. 63) and three cross-shaped chromosomes from another are illustrated (Pl. VIII, Fig. 64). Sax and Humphrey (1934) observed, in Tradescantia, that during metaphase the coiled chromatids of each chromosome gradually separate until each homologue consists of two separately coiled threads. In the present material, not only do sister chromatids lie parallel in independent spirals, as described by Kuwada (1938) in *Tradescantia reflexa*, but sister chromonemata are also side by side before metaphase. The four chromonemata of each dyad are so arranged that when viewed laterally they appear as two. When there is a twisting, however, especially

at the ends of the chromosome arms, the four-strand condition can be clearly seen (Pl. VIII, Fig. 63a–b; Pl. III, Fig. 20a, f, h).

The metaphase chromosomes have major and minor spirals. The major coils gradually increase in diameter as karyokinesis proceeds. Coiling appears to be unidirectional on a given side of the spindle attachment. The minor spirals are too small to be studied in detail. As the two dyads of the rings gradually separate they disjoin first at the distal ends of the short arms and then at the distal ends of the longer arms (Pl. III, Fig. 20a–g). One ring-shaped tetrad has two constrictions, one apparently the fiber-attachment constriction, the other subterminal and usually disappearing in later stages (Pl. VII, Fig. 57). Six submedianly constricted dyad chromosomes are formed from the metaphasic ring tetrads (Pl. III, Fig. 19; Pl. VII, Fig. 57). The dyads from each cross-shaped tetrad are rodlike or have almost terminal constrictions (Pl. III, Fig. 20h–j). A side view of this stage is shown in Plate VII, Figure 58. The sister chromatids of each dyad separate distally but are still held together at the fiber-attachment region (Pl. VII, Fig. 59). Each half dyad consists of two double-coiled chromonemata.

3. *Anaphases.* — The anaphase chromosomes move into mirror-image positions at the poles (Pl. VII, Fig. 60). During anaphase eight chromonemata in each geminus become discernible (Pl. VIII, Fig. 65). The major coils are more definite: five in the long arms of the chromosomes with submedian constrictions and of those with subterminal ones; three in the short arms of the submedianly constricted chromosomes. Generally one or two chromosomes reach the poles before the others (Pl. VII, Fig. 60).

4. *Telophases and interphase.* — During telophase sister chromatids become parallel, and the four chromonemata interconnect; a reticulum arises; and the minor coils of the chromonemata gradually lose their identity (Pl. VIII, Fig. 66). Individual chromosomes now appear, very much as they did at diakinesis, the chromonemata being arranged in the same manner as they were then (Pl. VIII, Fig. 69). Later stages exhibit a looser reticulum, involving a multitude of apparently threadlike interconnections between chromosomes (Pl. VIII, Fig. 67); individual chromosomes remain recognizable. The chromosomes gradually become strongly stainable and compact masses (Pl. IX, Fig. 70).

B. *Second Meiotic Division*

1. *Prophases.* — As prophase of the second meiotic division begins, the chromosomes unravel from the compact masses; this process is accompanied by a progressive loss of stainability. They then expand, become more uniform in diameter, and finally spread evenly throughout the nucleus as loosely coiled threads (Pl. IX, Fig. 71). In later stages it is not impossible to trace each chromosome for its whole length (Pl. IX, Fig. 72), and all chromosomes in a single nucleus may be analyzed. The split chromosomes have threadlike connections at the fiber-attachment region; distal regions diverge. Chromosome structure and behavior here are much like those observed by Taylor (1931) in Gasteria. In the present material three chromosomes are submedian and three are subterminal, one of the latter bearing a pair of satellites. No satellites or subterminal fiber attachments were found in the chromosomes of the first meiotic division; they were probably obscured by the extreme thinness of the chromonemata and the abundant matrical substance.

Taylor (1931) found, in Gasteria, that a splitting takes place at late prophase of the second meiotic division. In the material studied by the writer the splitting of each of the chromatids was seen to take place at late diakinesis and was traced to the first telophase, where the two pairs of chromonemata in each dyad merge into a reticular structure. This four-strand condition reappears optically at late prophase of the second division (Pl. IX, Fig. 73). Sister chromonemata at this stage are closely twisted about each other instead of being mutually parallel, as they were in the first meiotic division.

According to Nebel (1932a), in *Tradescantia reflexa* four chromonemata are evidently dyad chromosomes from the first telophase through the second prophase, where two double spirals are formed for every four chromonemata. The gyres of the double spirals correspond initially to those of the first meiotic chromosomes, but soon the two chromonemata of the double spiral are thrown into secondary spirals, which are very small. This seems similar to the condition observed in second prophase of the present material, though here the formation of secondary spirals probably takes place earlier. They are considered to occur at the end of the first telophase, when the chromosomes draw together and form compact masses. As the chromosomes emerge from these masses the two chromonemata

of each half dyad must be so closely entwined that they appear single at early second prophase. When the chromosomes contract and thicken, the duality is brought out again. With the reappearance of the secondary spirals the old coils gradually straighten (Pl. IX, Fig. 73). Only a few satellites were found (Pl. VIII, Fig. 61a; Pl. IX, Fig. 72).

As the process advances, the chromosomes greatly shorten and thicken and become differentiated into their constituent matrix and chromonemata. The number of secondary spirals is much reduced (Pl. IX, Fig. 74). The half dyads may or may not separate before the nuclear membrane disappears.

2. *Metaphase.* — As the nuclear membrane vanishes the dyad chromosomes draw close together into apposition and shorten somewhat (Pl. III, Fig. 21; Pl. IX, Fig. 75). They lie around the edge of the plate with their fiber-attachment regions toward the center. Kuwada and Nakamura (1935), in *Tradescantia reflexa*, observed the chromonemata at this stage to be singly coiled and parallel to each other. In the present material, however, they are intertwined, as described by Taylor (1931), Nebel (1932a), and others. The chromosomes of this division are essentially like those of a somatic division, though shorter.

3. *Anaphases.* — Anaphasic movement is assumed to be completed quickly and the daughter chromosomes oriented at the poles (Pl. IX, Fig. 76). Two polar views of the anaphase group are shown in Plate III, Figure 16. The anaphase chromosomes are usually less thick than the metaphase ones, but structurally they are the same. If examined by ordinary methods the internal structure of chromosomes at second metaphase and second anaphase is obscure. Their coiled nature and the duality of each half dyad is revealed more clearly by preliminary natural desiccation. The double nature of half dyads at second anaphase has also been described by Taylor (1931), in Gasteria, Nebel (1932a), in Tradescantia, Sax (1935), in Rhoeo, and Kuwada and Nakamura (1935), in Tradescantia.

4. *Telophases.* — The twisted condition of the chromonemata is still visible at telophase (Pl. X, Fig. 77). The chromosome mass becomes enveloped by a new membrane, the nucleus enlarges, and the chromosomes lengthen greatly (Pl. X, Fig. 78). The duality of each chromosome becomes clearly evident. As the process goes on, the chromosome outline is gradually lost, and eventually the chro-

matic structure spreads uniformly throughout the nucleus (Pl. X, Figs. 79–80).

Summary

1. *Spironema fragrans* shows six pairs of somatic chromosomes, of which three pairs are submedian and three pairs subterminal. One pair of the subterminal chromosomes bears satellites. Two pairs of the chromosomes are considered to be heteromorphic.

2. *Neodonnellia grandiflora*, with sixteen pairs of somatic chromosomes, shows two submedian pairs and fourteen subterminal pairs. Three pairs of the subterminal chromosomes bear satellites.

3. *Rhoeo discolor* appears to have six pairs of somatic chromosomes, with three pairs having an almost median fiber attachment and three pairs having a fiber attachment at one third of the distance from one end.

4. The somatic chromosomes in *Spironema fragrans* are double throughout mitosis and become quadruple in premetaphase. In meiosis the leptotene threads appear to be double. Division of the chromatids takes place in premetaphase of the first meiotic division. Each homologous chromosome at first metaphase consists of four chromonemata which appear as four independently double-coiled spirals. At anaphase each contains a pair of chromatids which part along their distal ends and hold together only at the fiber-attachment region. Each chromatid of the dyad consists of a pair of chromonemata which are parallel to each other, with their corresponding turns arranged at the same level.

5. At second meiotic division new spirals are formed which uncoil the relic spirals. The second metaphase and anaphase chromosomes are therefore composed of minor spirals only. The duality of the second anaphase and telophase chromosomes is clearly visible.

6. The behavior and the origin of the nucleoli in somatic telophase were studied in *Spironema fragrans*. The nucleolar material is considered to be collected at the fiber-attachment region of each chromosome, and the nucleoli were observed to be accumulated in the midst of, or in the spaces between, the centromeres of the chromosomes. The relation between nucleolus and chromosomes was traced at prophase and metaphase in *S. fragrans* and *Rhoeo discolor*. The nucleoli are not particularly attached to the SAT chromosomes or to any certain chromosomes. The chromosomes were seen to have equal

chances of forming nucleoli at telophase, and likewise to have an equal chance of being attached to the nucleolus at prophase and metaphase. A migration of the nucleolus from the distal end of the short arm of the chromosome to that of the longer arm, as the mitotic process advances from prophase to metaphase, was observed in *S. fragrans*. It is believed that the nucleolar substance contributes to the matrix of the chromosomes.

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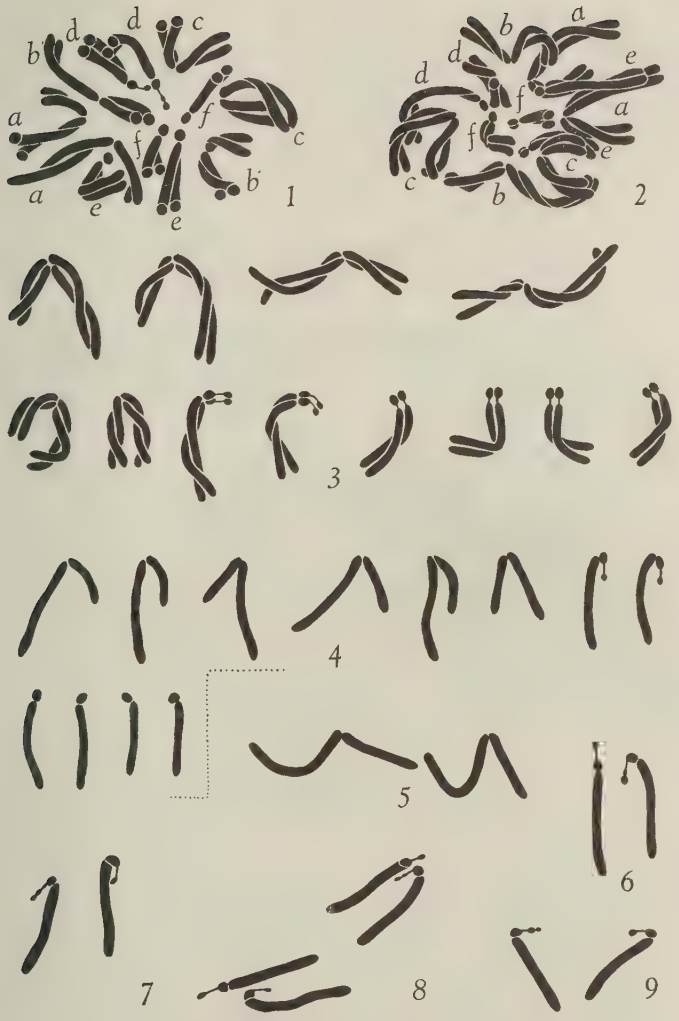
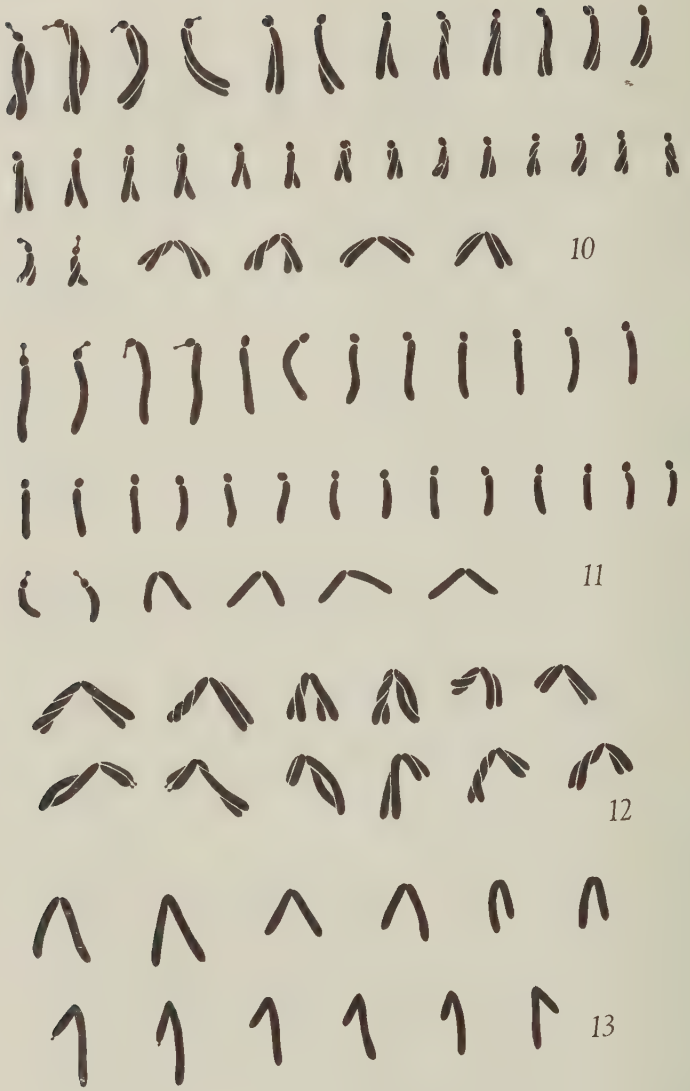
PLATES I–X



FIGS. 1–9. Chromosomes of *Spironema fragrans*. × 2000



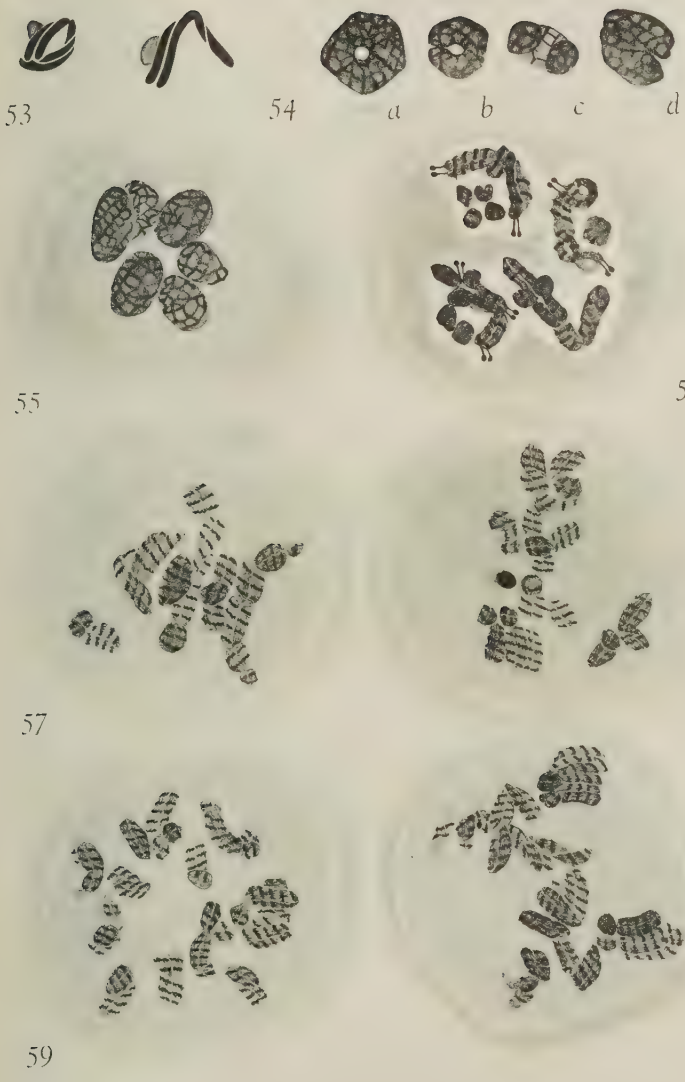
FIGS. 10–13. Chromosomes of *Neodonnellia grandiflora* (Figs. 10–11) and *Rhoeo discolor* (Figs. 12–13). × 2000

FIGS. 14–21. Chromosomes of *Neodonnellia grandiflora* (Figs. 14–15), *Rhoeo discolor* (Figs. 17–18), and *Spironema fragrans* (Figs. 16, 19–21). × 2000 except Figure 17 (× 1600)

FIGS. 22–31. Prophase chromosomes of *Spironema fragrans* (Figs. 22–27, 29–31) and *Rhoeo discolor* (Fig. 28). × 2000 except for Figures 30–31 (× 2800)

FIGS. 32–41. Chromosome development in *Spironema fragrans*. Figures 32, 34, 36, 40–41, × 2000; Figures 33, 37, × 2800; Figures 35, 38–39, × 2400

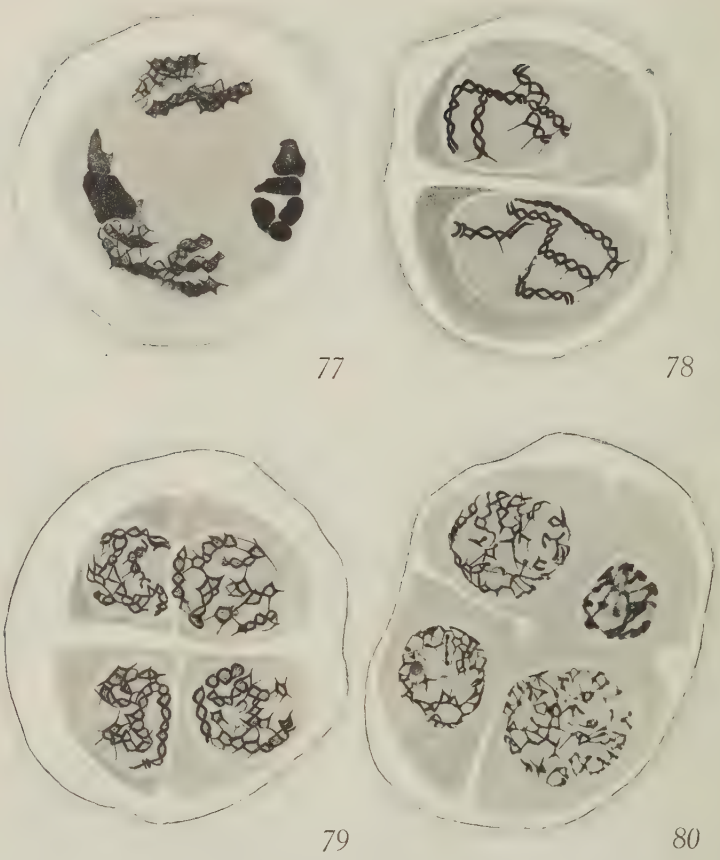
FIGS. 42–52. Nucleolus–chromosome relation in *Spironema fragrans* (Figs. 42–49) and *Rhoeo discolor* (Figs. 50–52). × 2000



FIGS. 53–60. Meiosis in *Rhoeo discolor* (Fig. 53) and *Spironema fragrans* (Figs. 54–60). × 2000

FIGS. 61–69. Meiosis in *Spironema fragrans*. × 2000

FIGS. 70–76. Meiosis in *Spironema fragrans*. × 2000



FIGS. 77–80. Meiosis in *Spironema fragrans*. × 2000

FORESTRY

SOME RESUPINATE POLYPORES FROM THE REGION OF THE GREAT LAKES. XIII *

DOW V. BAXTER

EMPHASIS on aviation in recent years has focused attention on types of wood appropriate for training planes and plane parts. Among the softwoods the spruces are the most valuable for such construction. Sitka spruce, *Picea sitchensis* (Bong.) Carr., is of prime importance because of the amount of clear lumber that can be obtained from healthy individuals. On the other hand, white spruce, *P. glauca* (Moench.) Voss, though it is a suitable material, is but little used in planes because it does not yield the necessary large quantities of clear lumber.

The value of recognizing the fungi which cause defect in spruce wood is apparent, but, except for certain conspicuous species such as *Fomes pini* (Thore.) Lloyd, *F. laricis* (Jack.) Murr., *Polyporus Schweinitzii* Fr., and *Pol. sulphureus* (Bull.) Fr. studied by Boyce (5), it seems that the common fungi on both Sitka and white spruce have not been critically investigated.

Recently, however, *Trametes serialis* in wood shipped from western North America has received attention abroad and also in the products' laboratories of this continent. Even though the fungus is frequent on spruce timbers little is known of its extent and occurrence in the regions where much of our spruce grows. The collections reported later in the present paper indicate that it has a wide distribu-

* Throughout the work on these monographs I am indebted to many institutions and individuals for help. My appreciation is expressed to Professors T. G. Halle and Gunnar Samuelson, of Naturhistoriska Riksmuséet in Stockholm, with whom I have had the pleasure of association. Thanks are also due the staffs of the Division of Pathological and Mycological Collections and the Division of Forest Pathology of the United States Department of Agriculture. I am under obligation, also, to Professor Walter H. Snell, of Brown University. Particular acknowledgment is made to the men who have accompanied me on my several expeditions to Alaska, the Yukon Territory, and the Northwest Territories. Much credit is due them for aiding in the collection and care of specimens and for living, at times, under rather difficult circumstances.

tion in both the coastal and the interior forests of Alaska, the Yukon Territory, and the Northwest Territories.

These collections were gathered in the course of a comparative study of the resupinate polypores of the continent, and, consequently, no effort was made to investigate specifically the relative abundance of the spruce-inhabiting resupinates with reference to the incidence of such fungi as *Fomes pini* and *Polyporus Schweinitzii;* yet the records do make it clear that they are plentiful enough to be considered in any study of the rots of spruce woods. Furthermore, since the data are based merely on random samples obtained on the several expeditions from 1932 to 1941 they suggest an even greater abundance of the fungi actually present in the areas.

A number of the species which decay spruce wood are not, however, important agencies of rot in the standing trees, although *Trametes serialis,* one form at least, causes considerable defect in both standing and down redwood. It is not known whether it occurs in other trees which attain large size, but its importance is recognized in structural timbers, particularly in Sitka spruce. Whether *T. serialis* developing in Douglas fir during transit is due to infection in the forest tree or in the wood after the tree is felled is a question which will undoubtedly receive attention in the future.

Trametes serialis is often entirely resupinate in its growth habits. Certain other closely allied polypores frequently resupinate on spruce wood are difficult to separate from *T. serialis* and have been more than once identified as that plant. This paper deals with *T. serialis* and *T. alaskana* and, in connection with them, discusses the related forms *T. heteromorpha* and *T. variiformis.*

Trametes serialis Fries, Hymen. Eur., p. 585. 1874

(Plate I, Figure 1; Plates III–IV, IX)

Polyporus serialis Fries, Syst. Myc., 1: 370. 1821.
Polyporus callosus Fries, *ibid.*, p. 381.
Polyporus scalaris Pers., Myc. Eur., 2: 90. 1825.
Poria callosa (Fr.) Sacc., Syll. Fung., 6: 298. 1888.
Coriolellus serialis (Fr.) Murr., N. Am. Fl., 9: 29. 1907.
Poria Sequoiae Bonar, Journ. For., 29: 377. 1931.

Fructification coriaceous, effused-reflexed or resupinate, laterally confluent, frequently for as much as 2.5 feet; surface of pileus "appressed-tomentose, zonate 0–2 × 1–38 × 3–0.8 cm."; margin thin, acute, undulating to lobed, concolorous; margin of

resupinate plants tomentose, up to 1 mm. wide, sterile at first, becoming fertile with age, white to "ivory-yellow" to "honey-yellow"; subiculum white, less than 1 mm., and mostly less than 0.5 mm., thick; tubes 1–8 mm. long, often oblique; mouths white or "ivory-yellow," to "honey-yellow" to "buckthorn-brown" in old specimens, but usually white or white to yellowish and retaining this color in herbarium specimens, circular to angular, 2–4, mostly 2–3, to a mm.; basidia hyaline, (5) 9–13 × 4–5.5 μ; spores smooth, hyaline, cylindric-ellipsoid, 7–9 × 2–3 μ,

Fig. 1. Distribution of *Trametes serialis* Fr. north of Vancouver
● = one collection
● = two or more collections

not guttulate; tramal hyphae smooth or incrusted, hyaline, apparently not branched, 3.5–4 μ in diameter; no clamp connections, no cystidia; chlamydospores appearing in cultures.

Allied species. — There are several resupinate polypores which are readily confused with *Trametes serialis.* The difficulties of diagnosis are increased if the collections come from southeastern Alaska and coastal British Columbia, since in those regions there is a plant, *T. alaskana,* sp. nov. (Pl. II), which bears many resemblances to *T. serialis.* This new species is much thicker and

has longer tubes and wider pore mouths than *T. serialis*. The greatest difficulty in separating the two plants will be experienced when *T. alaskana* is young, since then the mouths may be similar in size in both species. Even young specimens of *T. alaskana*, however, are thick, and the mouths and tubes become large. The two fungi may be distinguished readily in culture (see page 146).

If a pileus is present in *Trametes serialis* or *T. heteromorpha* these two polypores can be readily separated. The pileus of *T. serialis* is brown, not white as is that of the other fungus. Furthermore, the pore mouths of *T. serialis* average 2–4, mostly 2–3, to a mm., whereas those of *T. heteromorpha* are much larger, 0.5–3 to a mm.

In the United States, and particularly in the Central West, South, and Southeast, *Trametes Morganii* Lloyd is often labeled *T. serialis*. For the most part, the specimens on poplar and oak called *T. serialis* in herbaria throughout the country are actually *T. Morganii*. The comments of Lloyd (10) about the latter plant suggest relationships to *T. rigida* also: "Morgan referred it to *T. rigida*, a southern plant . . . ." Less confusion should exist, however, between *T. serialis* and *T. rigida* than between *T. Morganii* and *T. rigida*.

The fact that *Trametes Morganii* is not usually snow-white and that it occurs on hardwoods should be helpful in separating it from *T. serialis*. Furthermore, under most conditions *T. serialis* does not form a pore surface over as wide an area as does *T. Morganii*, though the lengthwise exteriors of both plants may be similar. Such a feature is, however, only relative and can be used merely to supplement other features in distinguishing the two plants. The spores of *T. Morganii* are $12 \times 6\ \mu$ according to Lloyd (10), but in my collections they correspond with those of *T. serialis*, which are $7–9 \times 2–3\ \mu$.

Trametes Morganii belongs to the "rapid-growth" [1] and "high-temperature" classes of fungi when placed in culture, whereas isolates of *T. serialis* grow more slowly and fall into the "medium" group for temperature of optimum growth.[2] Growth variations

[1] The terms used in this classification are defined in Papers V–VI (1–2) of the series.

[2] The Humphrey and Siggers (9) classification is: "Low-Temperature Group" (optimum 24° C. and below); "Intermediate-Temperature Group"

in culture of different isolates from separated geographical regions point, however, to the fact that data obtained from cultures cannot be relied upon entirely to distinguish these fungi, particularly if the collection comes from northern North America. Cultures are valuable only to furnish information supplementary to that based on the morphological features.

Misdetermined specimens of *Trametes malicola* B. and C. are found in herbaria under the name *T. serialis*. The pileus, context, tubes, and pore mouths of *T. malicola* are light brown, not whitish as in *T. serialis*.

Resupinate specimens of *Fomes fraxinophilus* Pk. (which do occur in dry locations) may be macroscopically similar to *Trametes serialis*. But in addition to the fact that the former species is always on white or green ash or on buffalo berry, bracket-shaped or knoblike immature fruiting bodies of the species are usually found elsewhere on the tree. The fruiting bodies of *T. serialis* are never on the outside of the trunk of a standing tree, although they are often found on the walls inside the so-called "goose pens" in living redwood. The large spore of *T. serialis* can be used to separate the plants, since the spores of *F. fraxinophilus* are ovoid and measure 5–6 × 6–7 μ.

The species of Fomes which has been most commonly confused with *Trametes serialis*, however, is *F. annosus*. Because this latter plant is found often in the resupinate condition and because it is white, leathery in texture, and occurs on conifers, it is easy to account for such incorrect identification. The spores of *F. annosus* are ovoid, measuring 4–6 × 3–4 μ, and so are different in shape and size from those of *T. serialis*. They readily distinguish the two plants.

In regions of much rainfall, southeastern Alaska in particular, *Fomes pinicola* is often seen in the resupinate form. In the early stages of growth for the plants of this area it has been mistaken for *Trametes serialis*. The thick growth also suggests that of *T. alaskana*, but in species of Fomes the pores remain small. In *F. pinicola* the pore surface characteristically turns pale brown where bruised; *T. serialis* does not exhibit this feature. The

(optimum 24° C. and 32° C.); and "High-Temperature Group" (optimum above 32° C.). Their isolate of *Trametes serialis* from Wisconsin falls in the "intermediate" group.

ovoid spores of *F. pinicola* are likewise distinctive when contrasted with the cylindric-ellipsoid ones of *T. serialis*.

Poria unitus (*P. medulla-panis*) also has been called *Trametes serialis*. Its spores are 4–7 (4 × 5) 3–6 μ and so differ from the large spores of this species of Trametes. The much-branched hyphae of *P. unitus* are also a feature of that plant.

In the Southwest *Polyporus anceps* Pk. often occurs in a resupinate state, and specimens from that region have been misdetermined and deposited in herbaria under the name *Trametes serialis*. Both plants appear on *Pinus ponderosa*, and it is usual for both to remain white after drying. But the spores of *Pol. anceps* measure 2–3.5 × 6–9 μ, whereas those of *T. serialis* measure 7–9 × 2–3 μ.

Old specimens of *Trametes serialis* may also suggest *Poria vaporaria*, particularly if the growth of the plant has been arrested somewhat during its development. The width of the spores of *P. vaporaria*, which are 5–6 × 1–2 μ, may be used to separate the two plants.

Poria sitchensis Baxter also suggests, macroscopically, a small-pored growth form of *Trametes serialis*. The spores of the latter plant, however, are much larger, 7–9 × 2–3 μ instead of 3.5–4.5 (4 × 1–1.5) 1–2 μ. In culture the white to brown nodulose growth of the mycelium of *P. sitchensis* is characteristic, whereas in all the many geographical isolates, including those from *Picea sitchensis*, the mycelium is white or whitish. Exudations from the mycelium are also a feature of *Poria sitchensis*. Furthermore, the two plants can be separated by the type of rot they produce in the host. The wood beneath the fruiting body of *Poria sitchensis* is whitish; that under *T. serialis* shows a brown, charcoal, or cubical rot.

Specimens of *Trametes serialis* that are in part pink, red, or even "Hay's lilac" are occasionally observed. I have collected many such discolored plants in the West and some in the Southwest and South, as well as in Sweden. The majority are old when found. These red but obviously once white fruiting bodies are to be seen in many herbaria. The change in color has led collectors to attach a variety of names to such specimens of *Trametes serialis*. Many are called, for example, *Poria sanguinolenta*. Even Bresadola interpreted one of his specimens of *T. serialis*

as *Polyporus incarnatus*. This red or violet color may be caused by a discomycete which is seldom found in the fruiting stage or by the mycelia of an imperfect fungus.

Habitat. — *Abies arizonica, A. balsamea, A. concolor, A. grandis, A. magnifica, Arbutus Menziesii, Betula papyrifera, Juniperus sp., Larix europa, L. laricina, L. occidentalis, Picea Engelmannii, P. glauca, P. pungens, P. rubra, P. sitchensis, Pinus contorta, P. flexilis, P. monticola, P. palustris, P. ponderosa, P. resinosa, P. Strobus, P. taeda, Pseudotsuga macrocarpa, P. taxifolia, Sequoia sempervirens, Taxodium distichum, Thuja plicata, Tsuga canadensis, T. heterophylla, T. Mertensiana.* Specimens are also reported on the hardwoods *Populus tremuloides, Quercus coccinea, Q. Prinus, Q. rubra,* and *Q. velutina,* but in all probability many of these plants are *Trametes Morganii.*

Distribution. — Alberta, British Columbia, Manitoba, Newfoundland, Northwest Territories, Ontario, Yukon Territory, Alaska, Arizona, Arkansas, California, Colorado, Connecticut, Georgia, Idaho, Illinois, Iowa, Kansas, Kentucky, Louisiana, Maine, Massachusetts, Michigan, Minnesota, Missouri, Montana, New Hampshire, New Jersey, New Mexico, New York, North Carolina, Ohio, Oregon, Pennsylvania, Rhode Island, Tennessee, Texas, Vermont, Virginia, Washington, West Virginia, Wisconsin, Wyoming.

Cultures. — Isolated from a cotton mill in Rhode Island and furnished by Professor Walter H. Snell. This fungus belongs to the "rapid-growth" group of resupinate polypores as well as to the "large-range" and "high-temperature" classes.

The optimum temperature for the germination of basidiospores in a culture from Madison, Wisconsin, was between 20° and 32° C., with the most rapid germination between 30° and 32° C., according to Snell (11). In his experiments the spores germinated at 30° but not at 40° C. This temperature is lower than that required for germination by such fungi as *Lenzites saepiaria, L. trabea, Lentinus lepideus,* and *Fomes roseus.* Some of the spores of this *Trametes serialis* isolate germinated after four years and three months. At 28° C. they ceased to germinate after an exposure of about ten weeks to dry incubator conditions, and at 36° C. most of the spores were killed within four weeks.

The hyphae form a white cottony mat in cultures on blocks

and finally cover the wood with a snow-white mass of mycelium. This conifer-inhabiting plant produces even greater masses of mycelium in cultures containing hardwood (red-gum) blocks or in flasks containing both red-gum and white-pine wood than it does in those with white-pine blocks. The fungus grows up and around the interior of a liter flask so as to fill much of the lower one third with mycelium. (This luxuriant growth is an important feature, and may be used to separate *Trametes serialis* from *T. alaskana*.) The habit of growth becomes nodulose, particularly in flasks which contain hardwood blocks. As the white mycelium ages it may darken in patches to "snuff-brown" or even to "Vandyke brown," and in some places it may form a brownish exudate. Abortive irpiciform and poroid fruiting bodies may appear on the nodulose portions of cultures which are six months to one year in age, and they develop in flasks containing either coniferous or hardwood blocks.

Decay. — Comparatively few fungi which inhabit coniferous wood cause such significant amounts of decay in both structural timbers and standing trees as does *Trametes serialis*. Both *Lenzites saepiaria* and *Poria incrassata*, for example, bring about enormous losses in coniferous structural wood, but they are of no economic concern in living trees, and though *P. vaporaria* in Europe has been recorded as an important cause of rot in wood structures and also in green trees in the forest, the records of such incidence in standing conifers cannot be regarded as authentic. The redwood form of *T. serialis* is one polypore which attacks coniferous wood both in slash or structural timbers and in the living tree (Pls. III–IV). In the Southwest *Polyporus anceps* Pk. on ponderosa pine slash and in living trees is another well-known example of a fungus which destroys down material and causes heart rot in standing timber.

Trametes serialis is best known in North America as the cause of a brown cubical rot of spruce and other coniferous logs and building timbers. Cartwright (6) describes its penetration in Sitka spruce and concludes that the cellulose of the cell wall is altered or consumed in advance by the fungus, so that actual penetration by the hyphal tip, which is partly mechanical, is facilitated. All except the finer hyphae are at first markedly constricted, but they soon resume normal size when the opposite

lumen is reached. Consequently, the bore hole is small at first and either may remain so or, after the cell wall is penetrated, may enlarge to many times the size of the hypha which formed it. The hypha in such a bore hole swells so that it no longer shows constriction. The mycelium in the wood has been revived after a dormant period of over seven and one-half years (8). This feature of resistance may possibly explain, in part, the frequent occurrence of *T. serialis* in buildings of certain types.

This fungus is an important agent of decay in storage yards in the Northwest. Lumber shipped abroad from mills in that region contained incipient decay of *Trametes serialis* which became apparent at the point of destination. Blair (3, 4) and Snell (11) report it, together with *Lenzites saepiaria*, *L. trabea*, and *Lentinus lepideus*, to be a source of decay in cotton-mill weave-shed roofs and basements in New England. It appears in flooring, in lumber yards, and in cabin timbers in Alaska. A "brown rot" of redwood exhibiting cubes that resemble those caused by *T. serialis* has been described, and a brown rot which breaks into cubes, apparently similar to that caused by *T. serialis* on coniferous blocks in culture, has been formed in cultures of the infecting fungus on wood. Spores of *T. serialis* from different localities show some variation in length, but, in general, are only one or two microns longer than those of *Poria Sequoiae*, described as causing a cubical rot of redwood. The spores of the latter fungus are given (7) as being 4.5–6 × 2–3.5 μ. The measurements recorded by various authorities for specimens of *T. serialis* are:

Murrill: 6–8 × 2.5–3 μ	Shope: 7–9 × 2–3 μ
Overholts: 7–8 × 2–3 μ	Bourdot and Galzin: 7–10 × 3–4 μ

Although the spores of *T. serialis* are usually 7–9 μ long, they occasionally exhibit considerable variation, i.e. from 6 to 10 μ, as indicated above. Those of a number of collections on different substrata in my herbarium show the following variations:

Host	*Spore measurements*
Lodgepole pine, Jasper, Alberta	5–6 × 2.5 μ
Sitka spruce, Skagway, Alaska	12 × 4 μ
Red spruce, Black Mountain, North Carolina	5–8 × 2–3 μ
Redwood, San Mateo, California	7–8 × 2 μ
Sitka spruce, Moose Pass (Grant Lake), Alaska	6.5–9 × 2–4 μ
White spruce, Great Slave Lake, Northwest Territories	5.5–7 × 2 μ

Trametes serialis is ordinarily more abundant on logs, on wood, and on structural materials in the coastal sections of Alaska than are such generally common plants as *Lenzites saepiaria* (Wulf.) Fr. and *T. odorata* (Wulf.) Fr. in the States. Environmental conditions in the southern areas of the Yukon Territory are dissimilar from those of the moist Pacific Coast of southeastern Alaska, and, consequently, *T. serialis* (among the polypores), though common in lodgepole and other conifers of the section, does not appear so abundantly as does *T. isabellina* Fr., a fungus frequently occurring on western and northern coniferous logs. My most northerly record for *T. serialis* in North America is from the Noatak River country north of the settlement of Kotzebue (north of Kotzebue Sound, Alaska).

In the Pacific Coast region of North America *Trametes serialis* results in a brown cubical rot in standing redwood. The decay suggests that in incense cedar caused by *Polyporus amarus*, except that in the advanced stages the pockets become so numerous or individually so large that they may constitute almost a solid mass of rot (7). The wood surrounding the cubes is dull brown, in contrast to the clear bright red or red brown of sound timber. Felts of white mycelium, which often become chalklike in age, frequently appear in the shrinkage cracks.

There is some correlation between the incidence of rot and the presence of fire scars. For decades and even for centuries ground fires have from time to time swept through the stands and exposed the aged heartwood in huge scars or goose pens. Such injuries provide points of entrance for *Trametes serialis* and indirectly lead to much cull caused by the fungus. The brown cubical rotted sections of the trunks are, in turn, more inflammable than is sound wood, and subsequent ground fires burn huge cavities in them. Fruiting bodies of *T. serialis* are often found on the walls of these goose pens.

Most of the rot appears to be in the first twenty feet from the ground, but the decayed areas sometimes extend through the second thirty-six-foot log. Decay also appears in the upper part of the trunk, but it has not been demonstrated as yet that it is caused by *Trametes serialis*.

That *Trametes serialis* is not known to cause decay in standing

timber of other species even in the same forest is a fact difficult to explain. Observations made on standing *Pseudotsuga taxifolia*, *Pinus monticola*, and *Abies grandis* growing in the redwood-forest areas have not revealed the presence of *T. serialis*, although the fungus attacks wood from these trees. But even old individuals of these species are much younger and smaller than redwood, so that there is less opportunity for the heartwood to become seasoned to the degree that it does in large specimens of Sequoia. Furthermore, resin accumulates over many of the wounds caused by fire in such associates and this may prevent infection. Redwood is not resinous and in old, immense specimens with large goose pens, it is probable that even the water-soluble extractives of the species which are toxic to fungi have leached out. Such a condition of the wood in the exposed old heartwood of standing trees may correspond in a general way, then, to that of wood in logs. Large specimens of *Thuja plicata*, *Libocedrus decurrens*, and *Chamaecyparis Lawsoniana* are also present in the northern areas of redwood, but these trees are neither so large nor so old as the Sequoia. Furthermore, they do contain oils which are often toxic to polypores.

Whatever the explanation may be for the incidence of the redwood form in standing trees, there is some relation between its occurrence and the presence of goose pens. Such large cavities, which are largely nonexistent in most other trees, may create internal atmospheric conditions more favorable for the growth of *T. serialis*.

Because goose pens result from repeated fires an effort should be made to prevent burning over redwood lands. It is believed that much cull can be eliminated in future stands by improving present methods of logging. The various types of high-lead steam skidding now in use cause excessive damage. The "slack-line" system employed by at least some companies leaves virtually no standing green timber on the land. Residual stands on adjacent areas logged over by tractor-arch units indicate that some progress can be made toward minimizing mechanical injuries and devastation. The undesirability of the custom of resorting to fire to rid a logged-over area of the débris incidental to the felling, limbing, and bucking operations is evident (7).

Trametes alaskana, sp. nov.

(Plate I, Figure 2; Plates II, V–VII)

Type and important specimens:

Trametes alaskana on *Picea sitchensis*, Cordova, Alaska, type. Coll. Dow V. Baxter, Aug. 21, 1933. Herb. Dow V. Baxter, Ann Arbor.

Trametes alaskana on *Picea sitchensis*, Sitka, Alaska. Coll. Dow V. Baxter, Sept. 1, 1933. Herb. Dow V. Baxter, Ann Arbor.

Trametes alaskana on structural timber beneath bank building, Valdez, Alaska. Coll. Dow V. Baxter, July 13, 1933. Herb. Dow V. Baxter, Ann Arbor.

Trametes alaskana on *Picea sitchensis*, Seward, Alaska. Coll. Dow V. Baxter, Aug. 14, 1933. Herb. Dow V. Baxter, Ann Arbor.

Fructificatio annua vel perennis, plus minusve 1 m. effusa, coriacea, usque 1.5 cm. crassa, resupinata vel semiresupinata, saepe nodulosa; margo primum sterilis, 1.5 cm. latus, plerumque minus quam 2 mm. latus, albidus vel pallide albidus, sed in crassis speciminibus, si margo non fit fertilis, brunneus; subiculum albidum; tubi plerumque 5–6 mm. longi, sed nonnumquam 22 mm. longi, saepe irpiciformes vel lamellati, albidi vel pallide ochracei; aperturae cum tubis concolores, 1–3, plerumque 1–2, in uno mm.; sporae hyalinae 10–12 × 3 μ; hyphae 2–4 μ diam., raro ramosae vel septatae.

Fructification annual or perennial, effused for 1 meter or less, coriaceous, up to 1.5 cm. wide, mostly less than 2 mm. wide, at first whitish, changing to "avellaneous" or, in thick specimens where the margin does not become fertile, "natal brown"; subiculum whitish; tubes mostly 5–6 mm., but up to 22 mm., long, frequently becoming irpiciform or lamellate, whitish to avellaneous; mouths concolorous with the tubes, 1–3, mostly 1–2, to a mm.; spores hyaline, 10–12 × 3 μ; hyphae 2 4 μ, seldom branched and seldom septate.

Allied species. — *Trametes alaskana* is allied to *T. serialis*, *T. heteromorpha* Fr., and *T. variiformis* Pk. These plants, in fact, are so closely related in some of their growth forms (particularly when in the resupinate state) that only with an abundant amount of material available in the field can some of them be distinguished accurately without the use of cultures. If it is possible to do so, one should obtain old as well as young material for representative samples.

For a number of years young plants of *Trametes alaskana* coming from coastal Alaska and having small tube mouths were ten-

tatively named *T. serialis* (Pl. V). Such young plants, however, are always thick and later have wide mouths.

Likewise, white or whitish specimens with wide mouths and a nodulose form of growth were tentatively referred to *Trametes heteromorpha.* Furthermore, specimens of *T. variiformis* which lacked pilei and which grew in similar habitats were confused with both *T. alaskana* and *T. heteromorpha.* Consequently, authentic material of Swedish plants has been studied in Sweden

Fig. 2. Distribution of *Trametes alaskana* north of Vancouver
● = one collection
● = two or more collections

as well as on this continent and numerous collections have been made. Cultures were obtained from certain specimens from widely separated localities, and the data from the cultures were matched with the morphological features of the fruiting bodies.

The thick habit of growth even in young specimens of *Trametes alaskana* should help to separate it from *T. serialis.* In addition, *T. serialis* often remains whitish in herbarium specimens, whereas the Alaskan plant discolors upon drying.

Mature specimens of *Trametes alaskana* and *T. variiformis* are similar in the size of the pores. *T. alaskana,* however, forms a

thick growth over the substratum, whereas *T. variiformis* forms a relatively thin one. The tubes of *T. variiformis,* although definitely coriaceous, are more paper-like and certainly less coarse (Pls. VIII–IX). Pilei are unknown in *T. alaskana;* in *T. variiformis* the pileus, if present, has a brown surface. An indication of this brown color can be detected at the margins even of many resupinate plants. Marginal growth is exceedingly irregular and wavy in *T. variiformis,* so much so that the plant frequently

Fig. 3. Distribution of *Trametes variiformis* north of Vancouver
● = one collection
● = two or more collections

occurs in small patches, often more or less circular, on a decorticated log, or in the checks of charred timber, rather than in long, rather wide, continuous sheets. This habit of growth, though noticeable in *T. heteromorpha, T. alaskana,* and *T. serialis,* is not so conspicuous in those species. Both *T. heteromorpha* and *T. alaskana* frequently exhibit a nodulose habit of growth.

The pileus of *Trametes heteromorpha* is white, and in resupinate specimens marginal portions may suggest the white of a pileus. Resupinate plants of *T. heteromorpha* appear in two different growth forms, one having long coriaceous tubes with thick dis-

sepiments (as in *T. alaskana*) and usually remaining white or whitish (Pl. X), and one having short somewhat irpiciform (or sinuous, as in *Poria sinuosa*) tubes and becoming "ochraceous buff," or at least not remaining whitish (Pl. XI). These forms may be distinguished from *T. alaskana* with long white tubes by the fact that the latter, instead of remaining white, exhibits brown discolorations in the upper marginal parts; and from *T. alaskana* with relatively short tubes, by the fact that *T. hete-*

Fig. 4. Distribution of *Trametes heteromorpha* Fr. north of Vancouver
● = one collection
● = two or more collections

romorpha remains white or whitish and has characteristically thinner dissepiments. Emphasis is to be placed always on the thick growth features of *T. alaskana.*

Habitat. — *Picea glauca, P. sitchensis, Tsuga heterophylla.* This species will probably be found in Douglas fir in British Columbia, Oregon, and Washington.

Distribution. — Yukon Territory, Alaska. This plant probably occurs also in British Columbia, northern California, Oregon, and Washington.

Occurrence. — *Trametes alaskana* is, in general, restricted to the

TABLE I

COLLECTIONS OF *TRAMETES SERIALIS* ON VARIOUS SUBSTRATA FROM NORTHERN NORTH AMERICA

(Herb. Dow V. Baxter)

Substratum	Form of timber	Locality	Expedition
Tsuga heterophylla...	Decorticated log	Sitka, Alaska	1933
Picea glauca.....	Decorticated log	Fort Wrigley, Northwest Territories, Canada	1937
.....	Decorticated log	Ruby, Alaska	1936
Picea glauca.....	Decorticated log	Nenana, Alaska	1936
Picea glauca.....	Decorticated log	Moose Pass, Alaska	1938
Picea glauca.....	Log with bark	Burnt Island, Great Slave Lake, Northwest Territories, Canada	1937
Pseudotsuga taxifolia	.....	Vancouver, British Columbia, Canada	1933
Picea sitchensis?....	Caps and posts used in tunnel supports	Tunnel, Alaska	1939
Picea glauca.....	Stack support in lumber yard	Fairbanks, Alaska	1936
Picea glauca.....	Decorticated log	Lower Russian Lake, Kenai Peninsula, Alaska	1936
Picea glauca.....	Decorticated log	Burnt Island, Great Slave Lake, Northwest Territories, Canada	1937
Pseudotsuga taxifolia	Decorticated log	Jasper, Alberta, Canada	1935
Picea glauca.....	Old lumber	Fairbanks, Alaska	1933
Picea glauca.....	Decorticated log	Waterways, Alberta, Canada	1937
Picea glauca.....	Decorticated log	Fort Smith, Northwest Territories, Canada	1937
Pinus contorta.....	Charred log	Jasper, Alberta, Canada	1935
Picea sitchensis.....	Decorticated log	Skagway, Alaska	1932
Picea glauca.....	Decorticated log	Dawson, Yukon Territory, Canada	1935
Tsuga heterophylla...	.....	Vancouver, British Columbia, Canada	1933
Pseudotsuga taxifolia	Decorticated log	Hope, British Columbia, Canada	1937

TABLE I (*Concluded*)

Substratum	Form of timber	Locality	Expedition
Picea glauca.....	Decorticated log	Tanana, Alaska	1936
Picea glauca.....	Log with bark	Burnt Island, Great Slave Lake, Northwest Territories, Canada	1937
Picea glauca.....	Old tramway timbers on 1898 trail	Whitehorse, Yukon Territory, Canada	1935
Picea sp.....	Base log in house	Fairbanks, Alaska	1940
.....	Decorticated log	Lake Louise, Alberta, Canada	1933
Picea glauca.....	Decorticated log (overgrowing specimen of *T. variiformis*)	Fairbanks, Alaska	1933
Picea glauca.....	Decorticated log	Beaver, Alaska	1935
Tsuga Mertensiana..	Discarded railroad ties	Fairbanks, Alaska	1933
Picea sitchensis.....	Decorticated log	Seward, Alaska	1933
Picea glauca.....	Decorticated log	Carcross, Yukon Territory, Canada	1932
Picea glauca.....	.....	Hot Springs, Alaska	1936
Picea sitchensis.....	Decorticated log	Seward, Alaska	1933
.....	Decorticated log	Grant Lake, Kenai Peninsula, Alaska	1938
Picea glauca.....	Decorticated log	50 miles south of Kotzebue, Alaska	1940
Picea glauca.....	Log with bark	Noatak River, 40 miles north of Kotzebue, Alaska	1940
Picea glauca.....	Decorticated log	Unalakleet, Alaska	1941

northwest coastal regions of the continent. Only two collections have been made elsewhere, one at Carcross, Yukon Territory, and one at Koyukuk, Alaska. The plant is found on structural timbers and decorticated logs.

Though a study was not made in the field to determine the abundance of the species and though collections were not taken of every specimen observed in the forests, the results of the random sample from the region north of Vancouver, British Columbia, of 146 collections in which *Trametes serialis*, *T. alaskana*, *T. variiformis*, and *T. heteromorpha* are present are of interest (see Figs. 1–4, pp. 141, 151–153, and Tables I–IV, pp. 154–156, 158–160). Sixty per cent of the collections of *T. alaskana* occur on Sitka

TABLE II

COLLECTIONS OF *TRAMETES ALASKANA* ON VARIOUS SUBSTRATA FROM NORTHERN NORTH AMERICA

(Herb. Dow V. Baxter)

Substratum	Form of timber	Locality	Expedition
Picea sitchensis	Decorticated log	Cordova, Alaska	1933
Tsuga heterophylla	Decorticated log	Ketchikan, Alaska	1933
Picea sitchensis	Decorticated log	Ptarmigan Lake, Kenai Peninsula, Alaska	1933
Tsuga heterophylla	Decorticated log	Wrangell, Alaska	1935
Tsuga heterophylla	Decorticated log	Cordova, Alaska	1933
Tsuga heterophylla	Decorticated log	Sitka, Alaska	1933
Tsuga heterophylla	Decorticated log	Sitka, Alaska	1933
Picea sitchensis	Decorticated log	Cordova, Alaska	1933
Picea sitchensis	Decorticated log	Seward, Alaska	1933
Picea sitchensis	Decorticated log	Cordova, Alaska	1933
Picea sitchensis	Decorticated log	Ketchikan, Alaska	1933
Picea sitchensis	Decorticated log	Mills Bay, Kodiak, Kodiak Island, Alaska *	1938
Picea sitchensis	Decorticated log	Skilak Glacier, Kenai Peninsula, Alaska	1938
Picea sitchensis	Reconstructed Russian blockhouse timbers	Sitka, Alaska	1939
Picea glauca	Decorticated log	Koyukuk, Alaska	1936
Picea glauca	Decorticated log	Carcross, Yukon Territory, Canada	1932
Picea sitchensis	Structural timber	Cordova, Alaska	1933
Picea sitchensis	Decorticated log	Hope, Alaska	1933
Tsuga heterophylla	Decorticated log	Wrangell, Alaska	1935
Picea sitchensis	Decorticated stump	Ketchikan, Alaska	1933
.....	Structural timber beneath bank	Valdez, Alaska	1933
Picea sitchensis	Decorticated log	Sitka, Alaska	1933
Picea sitchensis	Decorticated log	Sitka, Alaska	1933
Picea sitchensis	Decorticated log	Cordova, Alaska	1933
Picea glauca	Decorticated log	Lower Russian Lake, Kenai Peninsula, Alaska	1936
Tsuga Mertensiana	Decorticated log	Mole Harbor, Admiralty Island, Alaska	1941
Picea sitchensis	Decorticated log	Lost Lake trail, vicinity of Seward, Alaska	1941

* The most westerly collection in the North American coastal forest.

spruce, in contrast to eleven per cent of those of *T. serialis*. Eighteen per cent of all these species in the 146 collections are *T. alaskana*. At least sixty per cent of the entire group of plants occur on either *Picea sitchensis* or *P. glauca*, and seventy-one per cent of the specimens of *T. alaskana* are on spruce. *T. alaskana* and *T. heteromorpha* are more abundant on *P. sitchensis* than is either *T. variiformis* or *T. serialis*. *T. heteromorpha* is more likely to appear on wood with bark than *T. alaskana* or any other of these fungi.

Cultures. — Isolated from *Trametes alaskana* on *Picea sitchensis*, Kodiak Island, Alaska; the specimen was collected at the extreme limits of the coastal coniferous forest of the continent. Another Alaskan isolate of this same variety came from Sitka-spruce stringers in a mill yard, Juneau, Alaska.

It is usual for isolates made from various sources to differ, but these Alaskan plants are members of a growth group dissimilar from that into which *Trametes serialis* falls. Both isolates belong to the "slow-growth" group and the "small-range" and "average-temperature" classes.

Trametes alaskana grows much more slowly than *T. serialis*. The types of growth exhibited by the two fungi in culture also differ. *T. alaskana* (isolate from Juneau) does not form a thick enveloping growth over the wood in either white-pine or red-gum block cultures, but the mycelium of *T. serialis* in both hardwood and coniferous cultures almost completely hides the wood. This point is of interest, since in nature *T. alaskana* is the thick form. Nor does this fungus exhibit the conspicuous nodulose growth habit of *T. serialis*. Though both species formed tubes and pores in ten-month-old cultures on red-gum blocks, only *T. serialis* fruited in similarly aged cultures on pine blocks. Much longer tubes were produced in cultures of *T. alaskana* than in ones of *T. serialis*.

Cultures of *Trametes variiformis* (isolate from Toklat River, Mt. McKinley National Park, Alaska) are helpful in distinguishing it from both *T. alaskana* and *T. serialis*. Red-gum blocks are not hidden from view by *T. variiformis* even in two-year-old cultures. This feature suggests *T. alaskana* in culture. In contrast to the latter species, however, a nodulose growth (less luxuriant than that of *T. serialis*) is produced. Pore formation

TABLE III

COLLECTIONS OF *TRAMETES VARIIFORMIS* ON VARIOUS SUBTRATA FROM NORTHERN NORTH AMERICA

(Herb. Dow V. Baxter)

Substratum	Form of timber	Locality	Expedition
Picea glauca	Decorticated log	Mile 6, Mt. McKinley National Park, Alaska	1933
Picea glauca	Decorticated log	Toklat, Mt. McKinley National Park, Alaska	1933
Tsuga sp.	Decorticated log	Ptarmigan Lake, Kenai Peninsula, Alaska	1933
Picea sp.	Decorticated log	Tanana, Alaska	1936
Picea glauca	Decorticated log	Lower Russian Lake, Kenai Peninsula, Alaska	1936
Picea glauca	Decorticated log	Carcross, Yukon Territory, Canada	1932
Picea glauca	Decorticated log	Mt. McKinley National Park, Alaska	1932
.....	Decorticated log	Carcross, Yukon Territory, Canada	1932
Pinus contorta	Decorticated log	Lake Louise, Alberta, Canada	1933
Picea glauca	.....	Koyukuk, Alaska	1936
Picea sitchensis	Decorticated log	Moose Pass, Alaska	1933
Pinus contorta	Decorticated log	Jasper, Alberta, Canada	1935
Picea glauca	Decorticated log	Sheep Creek, Alaska	1935
Picea glauca	Decorticated log	Sitka, Alaska	1933
Picea sitchensis	Decorticated log	Seward, Alaska	1935
Picea glauca	Decorticated log	Koyukuk, Alaska	1936
Pinus contorta	Decorticated log	Jasper, Alberta, Canada	1935
Picea glauca	Decorticated log	Carcross, Yukon Territory, Canada	1932
Picea glauca	Decorticated log	Fort Smith, Northwest Territories, Canada	1937
Picea sitchensis	Decorticated log	Moose Pass, Alaska	1938
Picea glauca	Decorticated log	Koyukuk, Alaska	1936
Picea glauca	Decorticated log	Fort Wrigley, Northwest Territories, Canada	1937
Picea glauca	Decorticated log	Koyukuk, Alaska	1936
Picea glauca	Decorticated log	Burnt Island, Great Slave Lake, Northwest Territories, Canada	1937
Picea sitchensis	Decorticated log	Seward, Alaska	1933
.....	Decorticated log	Lower Tanana River (east of Tanana), Alaska	1936

TABLE III (*Concluded*)

Substratum	Form of timber	Locality	Expedition
.....	Charred log	Carcross, Yukon Territory, Canada	1932
.....	Charred log	Skagway, Alaska	1932
Picea glauca.....	Decorticated log	Sheep Creek, Alaska	1935
Picea sp.....	Decorticated log	Stillwater Crossing, Alaska	1936
.....	Decorticated log	Dawson, Yukon Territory, Canada	1935
Picea glauca.....	Decorticated log	Selkirk, Yukon Territory, Canada	1935
.....	Decorticated log	Ptarmigan Lake, Kenai Peninsula, Alaska	1933
Picea sitchensis.....	Charred log	Hope, Alaska	1933
Pinus contorta.....	Charred log	Skagway, Alaska	1932
Pinus contorta.....	Charred log	Jasper, Alberta, Canada	1935
Pinus contorta?.....	Decorticated log	Lake Louise, Alberta, Canada	1933
.....	Charred log	Carcross, Yukon Territory, Canada	1932
Tsuga heterophylla....	Decorticated log	Wrangell, Alaska	1935
Picea sitchensis.....	Decorticated log	Moose Pass, Alaska	1936
Picea glauca.....	Decorticated log	Selkirk, Yukon Territory, Canada	1935
Picea glauca.....	Charred log	Carcross, Yukon Territory, Canada	1932
.....	Decorticated log	Selwyn, Yukon Territory, Canada	1935
Picea glauca.....	Decorticated log	Mt. McKinley National Park, Alaska	1933
Picea glauca.....	Decorticated log	Lower Russian Lake, Kenai Peninsula, Alaska	1936
Pinus contorta.....	Decorticated log	Carcross, Yukon Territory, Canada	1932
Picea glauca.....	Decorticated log (overgrowing specimen of *serialis*)	Fairbanks, Alaska	1933
Picea glauca.....	Decorticated log	Selkirk, Yukon Territory, Canada	1935
Pinus contorta.....	Charred log	Skagway, Alaska	1932
Picea glauca.....	Decorticated log	Noatak River (Kotzebue Sound vicinity), Alaska	1940

TABLE IV

COLLECTIONS OF *TRAMETES HETEROMORPHA* ON VARIOUS SUBSTRATA FROM NORTHERN NORTH AMERICA

(Herb. Dow V. Baxter)

Substratum	Form of timber	Locality	Expedition
Picea sitchensis	Decorticated log	Juneau, Alaska	1936
Tsuga Mertensiana	Decorticated log	Cordova, Alaska	1933
Tsuga heterophylla	Log with bark	Wrangell, Alaska	1935
Picea sitchensis	Decorticated log	Seward, Alaska	1933
Tsuga Mertensiana	Decorticated log	Cordova, Alaska	1933
Picea sitchensis	Log with bark	Hope, Alaska	1933
Picea sitchensis	.....	Sitka, Alaska	1933
Picea glauca	Decorticated log	Toklat, Mt. McKinley National Park, Alaska	1933
Tsuga heterophylla	Log with bark	Sitka, Alaska	1933
Tsuga Mertensiana	Log with bark	Hope, Alaska	1938
Picea sitchensis	Log with bark	Juneau, Alaska	1936
Picea glauca	Decorticated log	Birch Lake, Alaska	1940
Salix sp.	Limb with bark	Birch Lake, Alaska	1940
Tsuga sp.	Log with bark	Skagway, Alaska	1932
Picea sitchensis	Log with bark	Juneau, Alaska	1936
Tsuga heterophylla	Decorticated log	Ketchikan, Alaska	1933
Tsuga Mertensiana	Log with bark	Hope, Alaska	1933
Picea sitchensis	Log with bark	Lawing, Alaska	1936
Picea glauca	Log with bark	Nenana, Alaska	1936
Picea glauca	Decorticated log	Sitka, Alaska	1933
Picea sitchensis	Log with bark	Uzinki (Kodiak Island group), Alaska	1938
Picea glauca	Log with bark	Fort Wrigley, Northwest Territories, Canada	1937
Tsuga Mertensiana	Log with bark	Ptarmigan Lake, Alaska	1933
Picea sitchensis	Limb with bark	Lower Russian Lake, Kenai Peninsula, Alaska	1936
Populus balsamifera (growing with *Picea glauca*)	Decorticated limb	Fort Wrigley, Northwest Territories, Canada	1937
Picea glauca (growing with *Populus balsamifera*)	Log with bark	Fort Wrigley, Northwest Territories, Canada	1937
Tsuga sp.	Log with bark	Seward, Alaska	1933
.....	Log with bark	Lower Russian Lake, Kenai Peninsula, Alaska	1936
.....	Snag with bark	Lawing, Alaska	1940
.....	Log with bark	Lower Russian Lake, Kenai Peninsula, Alaska	1936
Picea glauca	Log with bark	Lower Russian Lake, Kenai Peninsula, Alaska	1936
Tsuga Mertensiana	Log with bark	Hope, Alaska	1933
Picea glauca	Snag with bark	Lake Illiamna, Alaska	1941

resembling that of *T. heteromorpha* in nature appears in the cultures.

It is evident from these records that comparative studies of the species of Trametes in culture and of those of closely related genera are necessary. The variation that exists among isolates obtained from different regions makes such studies all the more imperative.

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PLATES I–XI

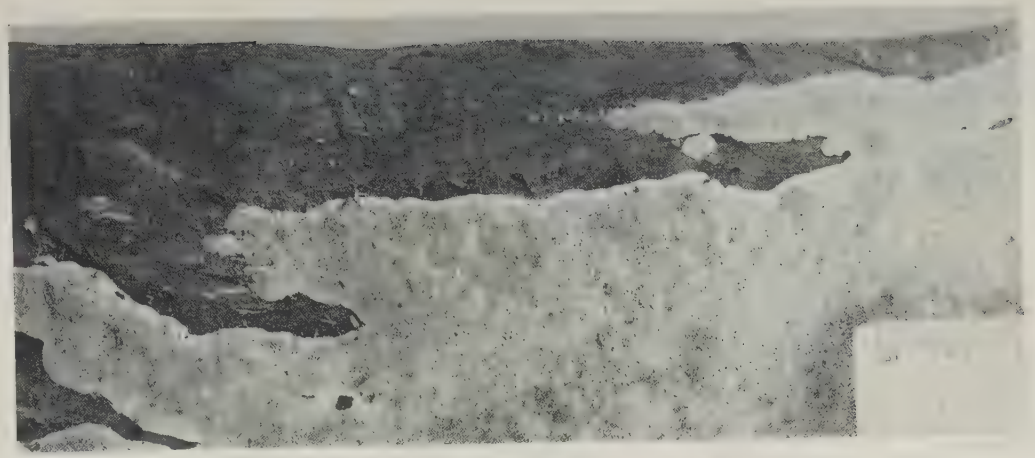


FIG. 1. *Trametes serialis* Fr., Moose Pass, Alaska, 1938

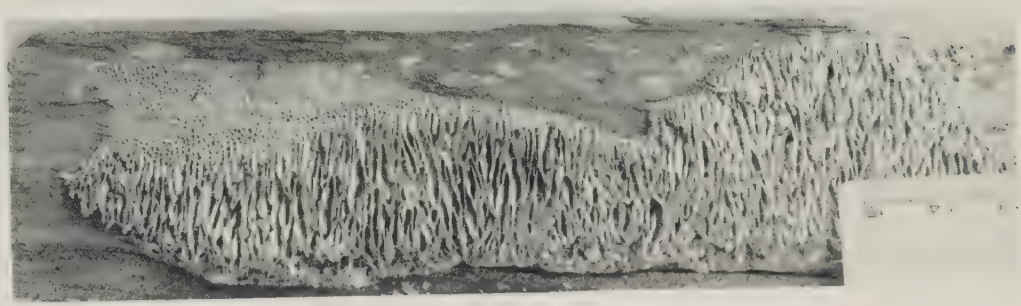
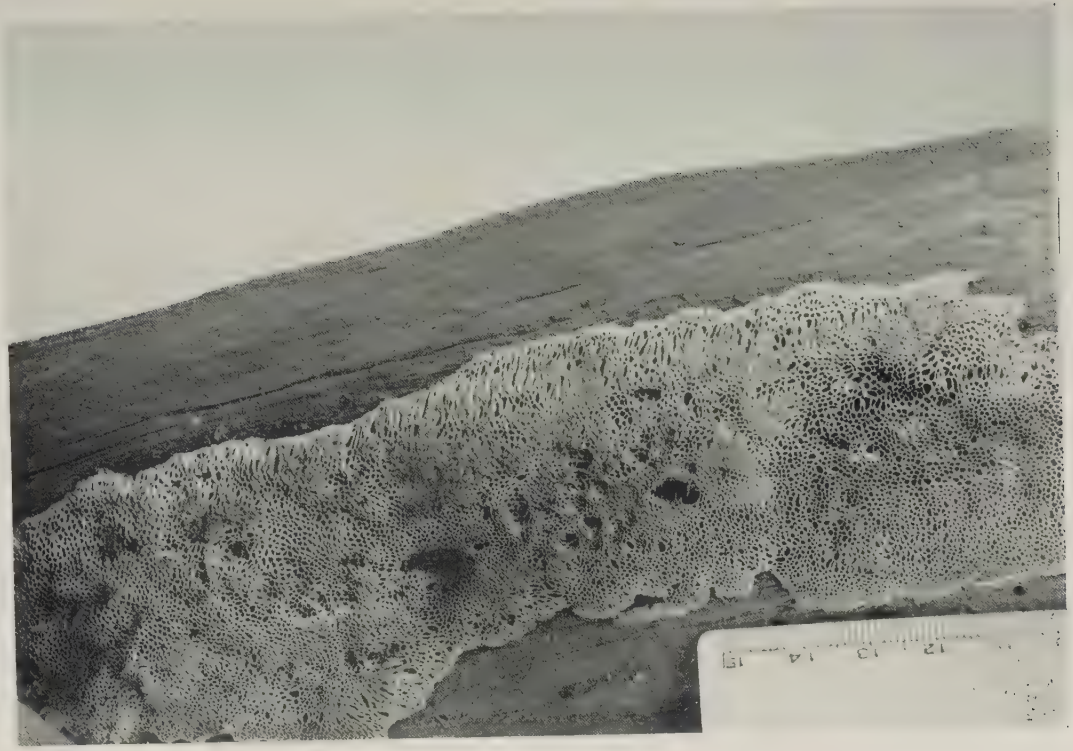


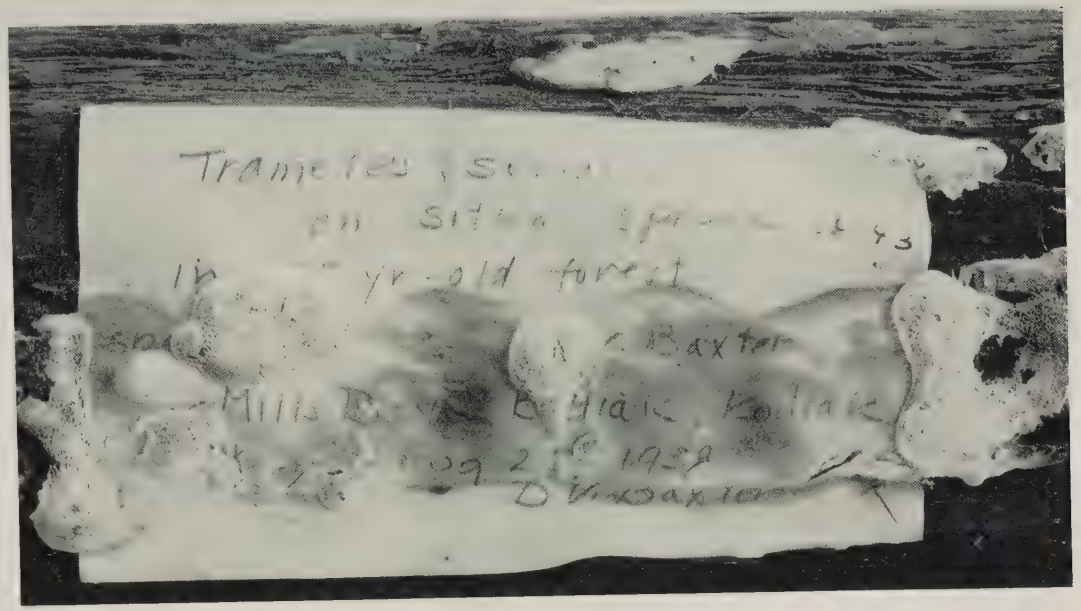
FIG. 2. *Trametes alaskana*, sp. nov., on *Picea sitchensis*, Seward, Alaska, 1933



Trametes alaskana, sp. nov., on *Picea sitchensis*, Sitka, Alaska, 1933

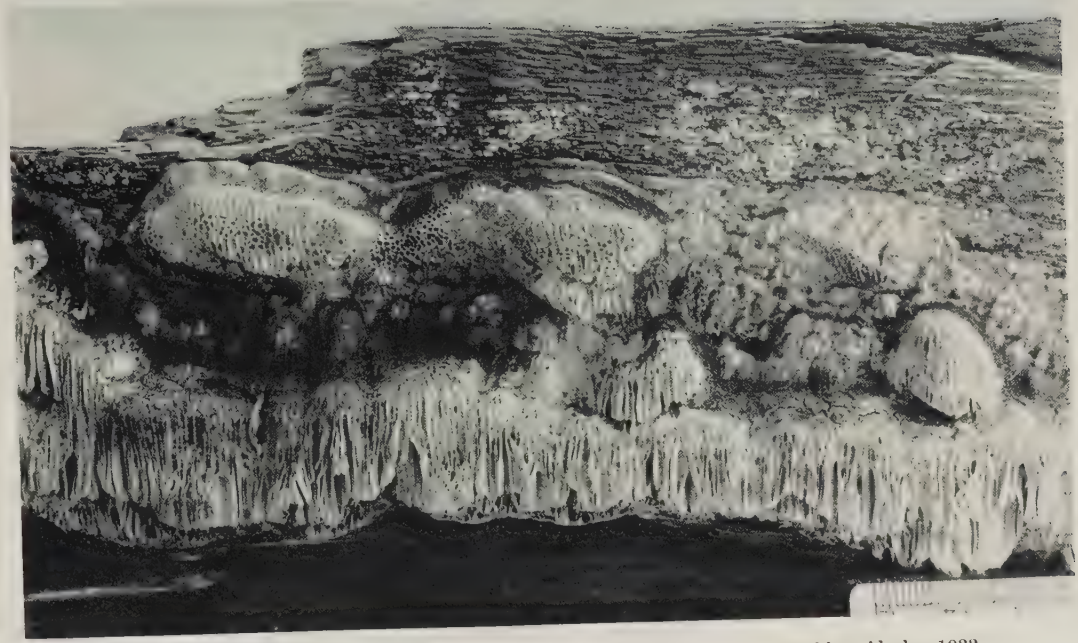
Trametes serialis Fr. (or a form of this species) on *Sequoia sempervirens*, Scotia, California

Rot caused by *Trametes serialis* Fr. (or a form of this species) in goose pen of redwood, Scotia, California



Trametes alaskana, sp. nov. (labeled *T. serialis* in field; see pp. 150–151), Mills Bay, Kodiak Island, Kodiak, Alaska. This collection was made at the limits of the coastal coniferous forest in North America. The fungus grew through the field label during transit to Ann Arbor. Thick growth habit and large pores are characteristic even of young plants

Trametes alaskana, sp. nov., on *Picea glauca*, Carcross, Yukon Territory. This is one of the few collections of this species from the interior forest regions of the continent (Carcross is just over the mountains from the coastal forest)



Trametes alaskana, sp. nov., on structural timber beneath bank building, Valdez, Alaska, 1933

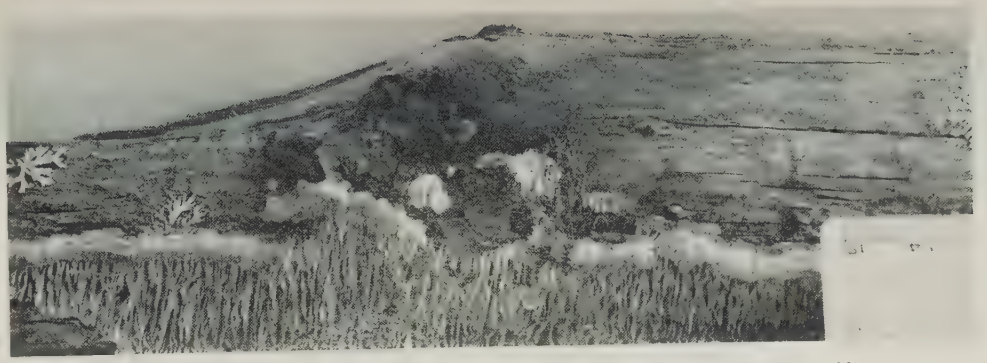
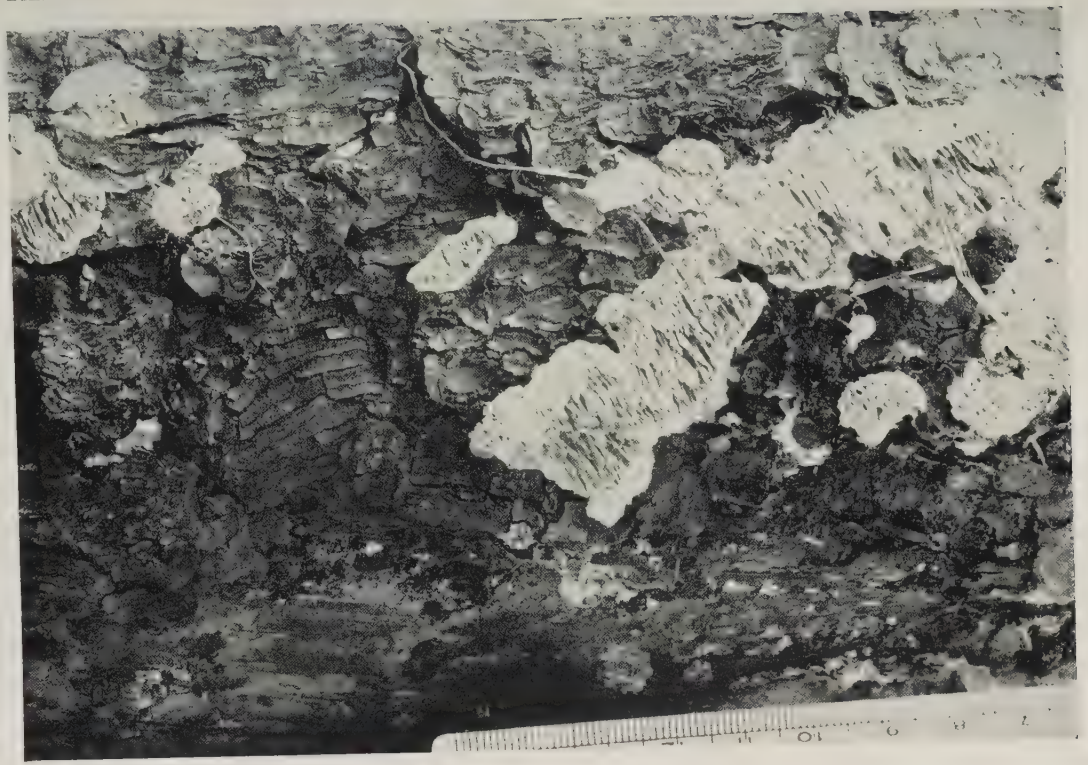


FIG. 1. *Trametes variiformis* Pk. on *Picea sitchensis*, Moose Pass, Alaska, 1933

FIG. 2. Resupinate *Trametes variiformis* Pk., Ptarmigan Lake, Kenai Peninsula, 1933. This fungus is more abundant on slash in this region than is *Lenzites saepiaria* (Wulf.) Fr.

Trametes variiformis Pk. (top of log) and *T. serialis* Fr. on *Picea glauca*, Fairbanks, Alaska, 1933



Resupinate *Trametes heteromorpha* Fr., Lower Russian Lake, Alaska

Resupinate *Trametes heteromorpha* Fr. on *Picea glauca*, Lower Russian Lake, Alaska.
In this stage of growth the fungus suggests *Poria sinuosa*

SAPWOOD IN SUGAR-MAPLE TREES

WILLARD S. BROMLEY

THE amount of sapwood in sugar-maple (*Acer saccharum*) trees has a direct bearing upon the price paid for the lumber obtained from them. The highest grades of sapwood lumber cut during winter, when the wood is whitest and is dried under special conditions, are sold for $20 more per thousand board feet than the best grades cut at other times. Even when the trees are cut in the summer and given no special drying treatment boards of the better grades with sapwood on just one side are sold for $10 more per thousand board feet than lumber of the same grade cut from the heartwood of trees. Although the presence or the absence of sapwood affects the price of sugar-maple lumber very materially, there is but little information in American literature concerning the width of the sapwood in the trees from which the lumber is sawed. It is the purpose of this paper to present the results of many measurements of maple trees and to discuss some of the factors which seem to affect the width of their sapwood. The results of similar studies made by German foresters and botanists are described by M. Büsgen and E. Münch, in *The Structure and Life of Forest Trees.*[1]

The data on which this study is based were compiled by C. B. Stott, of the Division of State and Private Forestry, United States Forest Service at Milwaukee, Wisconsin, from operations on two tracts of virgin northern hardwood timber in Michigan. One of them, in Baraga County, was cut in the summer of 1938; the other, in Iron County, in 1940. These records, which were loaned to the writer for analysis, show the diameter of heartwood, the width of sapwood, and the ages of more than two hundred trees at stump height.

The area in Baraga County contained trees of all ages on a site that is poor for sugar maple because of moist soil and inadequate

[1] Pages 121–129 of the translation by T. Thomson. New York: John Wiley & Sons, Inc., 1929.

drainage. This stand was composed of sugar maple, American elm (*Ulmus americana*), and yellow birch (*Betula lutea*), of equal importance in dominating the site. The area in Iron County had trees which seemed to be even-aged. This site is better for sugar maple, the dominant species, because it is higher and has better soil.

WIDTH OF SAPWOOD

The average width of sapwood at twenty-year intervals was obtained by deducting the average diameter of heartwood from that of the stumps measured. The remainder divided by two represented the average width of sapwood that is shown by age groups in Table I.

TABLE I

WIDTH OF SAPWOOD AND DIAMETER OF SUGAR-MAPLE STUMPS BY AGE GROUPS

Age group (years)	Timber all-aged, on poor site			Timber even-aged, on good site		
	No. of samples	Width of sapwood (inches)	Stump diameter (inches)	No. of samples	Width of sapwood (inches)	Stump diameter (inches)
120	14	4.7	13.3	..	..	..
140	6	4.5	13.6	..	..	..
160	2	4.3	14.5	2	5.3	13.9
180	14	4.3	16.1	12	5.9	17.1
200	21	4.4	18.2	16	6.7	19.9
220	13	4.7	20.2	16	7.1	21.8
240	16	4.9	22.0	3	7.5	23.3

It is evident that the width of sapwood is greater on the good site and that the greater width reflects the benefits of the better site even more than the sizes of the stumps at specific ages. On the poor site the average width was for all practical purposes relatively constant. Whether this is caused by the quality of the site or a characteristic of all-aged stands cannot be determined from the information collected. The sapwood in the older trees on the good site certainly shows a tendency to be wider. This may be due to the ability of the site to furnish water and nutrients in greater amounts as the trees become larger and older, so long as they maintain a dominant position in the canopy.

DECREASE IN PROPORTION OF SAPWOOD WITH AGE

It is well known that there is more sapwood in smaller and younger trees. The data compiled in the present study and recorded in Table II show this to be true even after trees reach merchantable sizes of twelve inches or more at breast height.

TABLE II

PERCENTAGE OF SUGAR-MAPLE STUMP AREA COMPOSED OF SAPWOOD

Age group (*years*)	*All-aged trees, poor site* (%)	*Even-aged trees, good site* (%)
120	91	..
140	88	..
160	84	94
180	78	92
200	74	89
220	71	88
240	70	87

These data are based on the cross-sectional area of the tree inside the bark at stump height. A greater proportion of sapwood is evident in trees on the good site, particularly in the older ones. It is reasonable to believe that the younger stands of timber on the more productive areas will contain more sapwood than those on poor sites. Lumber from sugar-maple trees grown on good sites will have greater value because it contains more sapwood. Although it is admitted that the younger and smaller trees have a larger proportion of sapwood, it does not necessarily follow that they will produce more valuable lumber than larger and older trees in the same stand.

INCREASE IN TOTAL AMOUNT OF SAPWOOD PER TREE WITH AGE

The small trees above the sapling stage have in their center many knots and imperfections which are included in the sapwood. As they grow older heartwood forms and gradually includes the knots or other defects while the tree annually puts on fresh layers of sapwood next to the bark. As the trees mature many of the dead limbs fall off the lower portion of the bole and eventually the sapwood becomes relatively free of knots. From then on the lumber from sapwood in mature trees is usually much clearer and freer of

defects than lumber from the sapwood in younger and smaller trees. Many lumbermen and foresters fail to appreciate this fact. Some become so impressed with the high proportion of sapwood in logs from younger trees that they cannot see that there is usually much more sapwood on the older trees. An indication of the manner in which it accumulates is given in Table III, which shows that the basal area of sapwood in the tree at stump height increases as the tree grows older.

TABLE III

Basal Area Per Tree of Sugar-Maple Sapwood at Stump Height

Age group (years)	*All-aged trees, poor site (square feet)*	*Even-aged trees, good site (square feet)*
120	0.88	. .
140	0.89	. .
160	0.95	0.99
180	1.11	1.45
200	1.33	1.93
220	1.59	2.29
240	1.84	2.57

The results are based on observations made of the stumps only. That the findings will apply in a general way to the entire merchantable portion of the tree has been established by measurements made at the small ends of more than five hundred sugar-maple logs cut in the Baraga County area. The records were compiled by the Forest Products Laboratory at Madison, Wisconsin, in an unpublished report dated February, 1940, and entitled "Alberta Log Grade Study." Although there were no data on ages in this report, it did show the same general characteristics for sapwood on the small ends of sugar-maple logs that have been noted for it at stump height of sugar-maple trees from the area in Baraga County.

In reviewing the field records on the observations of the stumps it was apparent that the width of sapwood is affected by factors other than those of age and site. Even on the poor site some stumps had sapwood widths of more than eight inches. It is likely that the location of a tree in a stand in reference to its competitors for light and soil moisture has a dominant effect upon the amount of sapwood retained by it. The combination of all the factors of site affecting a tree controls its rate of growth.

AMOUNT OF SAPWOOD AFFECTED BY RATE OF GROWTH

An inspection of the records of the stumps showing the greatest widths of sapwood revealed that they were usually associated with a rapid rate of growth. The greater the percentage of sapwood on a stump the smaller the number of years it took to grow one inch in diameter. This relation is evident in Table IV, which shows the average of all stumps observed. In it the average diameter of the heartwood also is given to show that the formation of heartwood and the reduction of the percentage of sapwood seem to be directly related to the decreasing rate of growth or the greater age of the trees.

TABLE IV

GROWTH OF SUGAR-MAPLE SAPWOOD AND DIAMETER OF HEARTWOOD

(Poor site, Baraga County, Michigan)

Age group (years)	No. of years to grow one inch	Percentage of stump area in sapwood	Diameter of heartwood (inches)
120	13.6	91	3.9
140	15.4	88	4.7
160	17.0	84	5.9
180	18.1	78	7.5
200	18.4	74	9.3
220	18.5	71	10.8
240	18.6	70	12.1

From the material in Table IV alone it seems reasonable to believe that, if the growth rate is kept high, a large proportion of sapwood can be retained in a tree, and an inspection of the records of individual trees indicates some basis for this opinion. Since second-growth stands have a high rate of growth and are not likely to reach the advanced age of our virgin forests of the past, one can expect higher percentages of sapwood in the next cut of sugar-maple trees of the northern hardwood forests. By maintaining these stands in a highly productive condition there will be even greater proportions of maple sapwood lumber in the future.

CONCLUSIONS

1. The width of sapwood was noted to be relatively constant at 4.5 inches in an all-aged stand on a poor site, regardless of the age

of the tree. On a good site and in an even-aged stand, however, the width of sapwood was greater, particularly on the older and larger trees.

2. The proportion of sapwood is greatest in the smaller and younger trees on both good and poor sites.

3. The total amount of sapwood per tree is greater in the larger and older trees.

4. The amount and width of sapwood are greater in the trees which have the highest rate of diameter growth. Foresters will therefore increase the production of sapwood in sugar-maple trees in the future by managing them so as to secure high rates of growth.

University of Michigan

PUBLIC FOREST HOMESTEADS

HENRY GILBERT WHITE

THIS paper deals primarily with the timber workers and settlers of the cutover region of the northern Lake States and with a program for improving their standards of living. Many of them are existing in the most abject poverty, in the midst of forest land and timber resources which, if properly handled, could supply them with an adequate income. A plan for Public Forest Homesteads is here proposed to help solve this problem. It is so called because it borrows what was good in the rugged, self-reliant life of early American homesteaders and adapts it to modern industrial society, where the individual cannot stand alone but must find security under public guidance.

In analyzing the viewpoints and experience which provide the setting for this plan it is necessary to go back into early United States Forest Service history. The conservation movement in the United States, which in the beginning was identical with the forestry movement, has always had broad humanitarian objectives. Since its transfer to the Department of Agriculture in 1905 the guiding principle of the Forest Service has been "the greatest good of the greatest number in the long run." [1] But this has been a long-term, nation-wide goal which has often drawn attention away from the immediate needs of local people for jobs and for timber products. Although the theory that the public forest should not be "locked up" for the sole use of future generations was accepted,[2] most of the early effort of the Forest Service was necessarily spent in protecting the forests from fire and illegal cutting. As rapidly as the pressure of other work allowed, it put into effect timber-sale and grazing policies permitting the maximum of private use not inconsistent with the interests of the general public. The enforcement of these policies

[1] Cameron, Jenks, *The Development of Governmental Forest Control in the United States*, p. 240. Baltimore: The Johns Hopkins Press, 1928.

[2] Pinchot, Gifford, "How the National Forests Were Won," *American Forests and Forest Life*, 36 (1930): 616.

often meant conflict even with local people until they became accustomed to the advantages of rules that prevented the destructive exploitation of the resources.

One of the first real tests of Forest Service policy came with the passage of the Forest Homestead Act of 1906.[3] This law was designed to correct injustices caused by the inclusion of agricultural land within Forest Reserve boundaries. Many western people had protested against the closing to settlement of this tillable land. Those with perfected titles to homesteads in the Forest Reserves complained of being denied neighbors on adjacent treeless land. Those with squatter rights found that they could not perfect their homestead titles because the surveying of lands in the Forest Reserves had been delayed in favor of needed surveys elsewhere.

The Forest Homestead Act of June 11, 1906, familiarly known as the "June 11" law, attempted to meet these criticisms by opening to homesteading any areas within the Forest Reserves which, on application to the Secretary of Agriculture, were determined to be "chiefly suitable for agriculture and might be so used without injury to the forest reserves." It was a just and well-drafted bill, but few anticipated the homestead hysteria and land-speculation fever that it released.

Within a short time after the passage of the "June 11" law thousands of applications for homesteads were filed with the Secretary of Agriculture. Probably a majority of them were not made in good faith, with the idea of tilling the land, but were attempts by private individuals and lumber companies to get title to valuable timberland. Nevertheless, each application was carefully appraised by the Forest Service in order not to prejudice the claims of legitimate settlers. It was a tremendous task of land zoning that had to be done under pressure of time and of individuals and groups with great political power. The Forest Service can justly be proud of the manner in which it handled this first real attempt at detailed land classification in the United States.[4]

Only five years after the passage of the "June 11" law the Forest Service was faced with the problems of unwise agricultural

[3] 34 Statutes at Large of the United States, 233.

[4] Sherman, E. S., "'June Eleventh' and Homestead Hysteria," *American Forests and Life*, 36 (1930) : 409; Ise, John, *The United States Forest Policy*, pp. 164–168, 254–261. New Haven: Yale University Press, 1920.

use of mountain land in the eastern and southern states. The Weeks Law of 1911[5] authorized the establishment by purchase of national forests east of the Mississippi. Often this meant buying up cultivated hillside farms and dispossessing the occupants. What happened to these people after their homes and lands were sold to the Government was not a primary concern of the Forest Service at that early date. According to the prevailing theory, it was assumed that they could and would seek better economic opportunities elsewhere.

It is not strange that the Forest Service, on the basis of these experiences, had a strong defensive complex against those who attempted to invade the pristine domain of the national forests. Settlers were expected to earn their entire income from farming. Widespread unemployment, agricultural depressions, and the full effect of disappearance of the western frontier had not yet suggested the need for more intensive use of the public forests to support destitute forest workers and settlers.

A similar policy of classifying land for its best use and, if that proved to be forestry, of moving the settlers out or, at least, of preventing further settlement, was later advocated and adopted in state and county land-zoning laws. The Wisconsin legislature passed the first rural land-zoning law in 1923. Its original purpose was to give the counties control over suburban land development. The authorization for counties to regulate the use of land for agriculture, forestry, and recreation was enacted in a 1929 amendment. The first county zoning ordinance under this amendment was adopted in 1933.[6] A few other states have similar zoning laws, but they have made less progress than Wisconsin.[7]

Rural zoning represents a very worth-while trend, with one important limitation. It assumes that settlers have only one objective and one source of income — farming. The need for part- or full-time forest workers and for homes for them in the forest has been entirely ignored. The zoning ordinance of Florence County,

[5] 36 Statutes at Large of the United States, 961.

[6] Rowlands, W. A., and Trenk, F. B., *Rural Zoning Ordinances in Wisconsin*, pp. 3–6. Circular No. 281 of the Extension Service of the College of Agriculture of the University of Wisconsin, July, 1931.

[7] Walker, Herman, *Problems and Suggestions in the Drafting of Rural Zoning Enabling Legislation*, pp. 4–7. Land Use Planning Publication No. 10. Resettlement Administration, Washington, D.C., December, 1936.

Wisconsin, reveals this deficiency.[8] It provides for three classes of use: forestry, recreational, and unrestricted. No family dwellings may be built in districts zoned for forestry. In the other two classes family dwellings are allowed. Thus a woods worker or part-time forest guard who must live near his work may be hard pressed to find a home site in an adjacent recreational or unrestricted district. If he secures such a site in a recreational district, he is prohibited from clearing land and farming. He must make his entire living from forestry work or recreation and, unless there is some wild-hay land available, he must buy all the feed for the horses he may need for logging and other work.

This situation may seem sensible to those who think of forestry in terms of reserving the forests for the use of future generations, but it does not conform to past experience or present-day needs. Throughout the history of the lumber industry in the Lake States logging has usually not been a full-time job. Many of the early lumberjacks had farms on which they worked during the summer months with the idea that they would eventually become full-time farmers. But experience has proved that a large number of the northern farms will never become self-sustaining. Their owners will always have to rely on woods work or other jobs to supplement their income.

In Sweden, where systematic forest organization has progressed further than in this country, the need for homesteads for woods workers located in or near public forests has long been recognized. As early as 1891 provision was made for leasing of homesteads to forest workers in one of the northern forested provinces. Each homesteader was given timber, free of charge, for building and other purposes, and also a grant of money. During the early part of each lease the homestead was rent- and tax-free. In return the homesteader was obligated to make good use of the site, serve as a forest guard, and work in the woods at the current wage.[9]

With certain modifications this system of encouraging settlement in northern forested Sweden has continued up to the present day. A royal decree of 1925 provided that homesteads should be granted only where "there is considered to be available supple-

[8] Rowlands and Trenk, *op. cit.*, pp. 34–39.

[9] The Royal Social Board, *Social Work and Legislation in Sweden*, Second revised English edition, pp. 273–275. Stockholm: Tryckeriaktiebolaget Tiden, 1938.

mentary work to enable the settler and his family to obtain the necessary subsistence. The settler is allocated 8 to 17 hectares of cultivable land, and besides as large an area of forest land as, with ordinary care and good management, will suffice to produce an annual supply of 15 to 20 cubic metres of timber. The lease is granted for 15 years. During the first ten years the settler is exempt from the payment of rent. . . . he enjoys certain grants from the State with no obligation to refund.

"For the buildings of his holding, the settler receives from the State a building grant of up to 3,500 kronor, in certain exceptional cases as much as 4,500 kronor. As a rule the settler himself takes in hand the erection of the buildings, but in certain cases the State takes charge of the work. Furthermore, the settler receives, free of charge, the building timber he requires, together with necessary fuel." [10]

In the United States the demand for full development of employment opportunities on public forests was not widely expressed until the depression years following the market crash of 1929. During these years foresters were among the first to invite the use of destitute settlers and unemployed workers in planting and improving devastated forest lands. In the beginning this solution of the problem was considered a temporary expedient for the relief of these people until their former sources of income should commence to flow again. Where the relief workers lived during this period was of no great concern to public officials. But as the need for relief work on the forests stretched from months into years it became apparent that the temporary government camps, the dilapidated cabins, and the tar-paper shacks which housed them were just as great a bar to their permanent rehabilitation as was the lack of an assured source of income.

In the forests of the northern Lake States several moves were made to establish permanent homesteads and improve existing ones for people needing relief. A comprehensive plan was prepared by the Forest Service in 1935 for the settlement and relocation of submarginal farmers and unemployed people on small tracts of farm land in or near the national forests.[11] It provided for loans and tech-

[10] *Ibid.*, pp. 275–276.

[11] Camp, John R., *A Plan for Social Adjustment for the Forest Areas of the North Central States, with Special Reference to the National Forests.* United States Department of Agriculture, Forest Service, 1935. (*Mimeographed*)

nical assistance in building up adequate homesteads. It was not expected that many of the settlers would be able to earn their whole living from farming; it was thought that most of their cash income would be derived from forestry work on the national forests. Homesteads were to be purchased over a long period of years through deductions from their cash earnings. The plan suggested that in some cases leasing of the homesteads rather than outright purchase would be advisable because it would place less of a burden on the settler and would provide a check on the wise use of the land.

The execution of this plan, at least in its entirety, was dependent, however, on large emergency relief appropriations, which were never forthcoming. It must be said to the credit of the Forest Service that, although appropriations were lacking for executing the 1935 plan, a number of less ambitious schemes for aiding the people of certain localities have been undertaken.

The Drummond project[12] on the Chequamegon National Forest in northwestern Wisconsin took some of the unemployed woodsmen and "shackers" left in the wake of a large-scale destructive logging operation, put them in new homes in a little forest community, and gave them part-time jobs in forestry work. Two important lessons were learned from this project: (1) that building houses with relief labor is expensive unless part of the cost is charged directly to relief, and (2) that forest communities should not be developed where there is little or no commercial timber unless no alternative exists or there is reasonable assurance of appropriations over a long period of years for planting and other forest-rehabilitation work. The ultimate goals should be self-liquidation of the investment in buildings and forestry work and self-sufficiency or financial independence of the homesteader.

The Chippewa National Forest of north-central Minnesota is better supplied with merchantable timber than the Chequamegon, and so has been able to inaugurate a program of reëmploying and rehabilitating settlers on an informal, coöperative basis. The first step has been to coördinate forest-management plans with the employment needs of the local people. Wherever possible, timber sales and forest-improvement work are allotted to local settlers. The Forest Service also assists by land exchange in the relocation of

[12] Other divisions of the United States Department of Agriculture as well as the Forest Service participated in this project.

settlers on better farm land closer to opportunities for work and community services.

Now that the Chippewa, Drummond, and other projects have tested the prospects and methods of rehabilitating the people of substandard income in the cutover region, the time seems ripe to inaugurate a plan for meeting and solving these problems on a permanent, region-wide basis. Several organizations[13] have recently attempted to focus public and legislative attention on the problems of the cutover region and the steps that might be taken to solve them. The Northern Lake States Committee report[14] shows that a decade of depression, relief appropriations, and desperate striving for recovery has not obliterated the effect of many decades of destructive exploitation of resources. If action does not result from these committee recommendations, it will be because their plans are not geared to fit present governmental trends, for many of them require larger relief appropriations than can possibly be obtained at the present time, when national and even local emphasis is shifting to military defense.

Artificial stimulation of business by defense expenditures may bring temporary prosperity to the extractive industries of the northern Lake States. Some of this money will trickle down to the woods workers and millmen, but very little of it will reach the submarginal. settlers. And when defense activities slacken the northern Lake States region may face a greater depression, with its resources more gutted than before.

This, then, is the time to adjust the economy of the region to withstand the shocks of industrial collapse. The region must tackle that problem in the face of declining relief appropriations. It has two resources with which to work: an abundance of forest land — poorly stocked, to be sure; and manpower, with its strength sapped by years of underemployment, but still lit with a spark of hope for a better way of life.

The plan here proposed to meet the challenge of this emergency is called "public forest homesteads" because it adapts the best fea-

[13] The Northern Lake States Regional Committee of the National Resources Committee and a Facilitating Interbureau Coördinating Committee of the United States Department of Agriculture.

[14] *Regional Planning, Part 7 — Northern Lake States.* Report of the Northern Lake States Regional Committee to the National Resources Committee. Washington: Government Printing Office, 1939.

tures in the life of the rugged pioneer homesteader to the requirements of the present day. Perhaps the name does not fully describe the comprehensive method by which the forest resources and industries of the region must ultimately be rebuilt to contribute most to the welfare and security of the local people. But it does indicate the central idea of providing permanent homes for woods workers who will protect and improve the forest and find security and happiness in a forest economy.

The essential features of the plan are these:

1. Local unemployed or underemployed people who are inadequately housed and have no land would be leased small tracts of tillable land (where available) and supplied with timber and other building materials at cost, often in exchange for labor, with which they could build themselves satisfactory homes. Settlers adequately supplied with land but with unsatisfactory buildings would be aided with building material and loans.[15] Settlers located inconveniently far from work opportunities and community organization should be relocated by land exchange, but not with the idea of depopulating the forest, upon which most of them are dependent for their cash income. In one way or another every settler should be provided with enough tillable land on which to grow much of the food needed for his family and his livestock. Although the cost of a subsistence homestead built up chiefly with a man's own labor should not be great, it would be unwise to require all settlers to buy their homesteads from the Government if they do not wish to do so or are financially unable. A long-term low-rate lease, terminable for good cause, would protect the rights and interests of both the lessee and the lessor — the latter being the Government in most cases.

2. Sufficient forest land should be dedicated to the use of each homestead or forest community to supply employment in harvesting the timber and to provide wood for home requirements.

Owing to the varying conditions and resources of each locality considerable flexibility would be necessary in budgeting available employment. In areas where the forests have been so thoroughly exploited and burned that there is little commercial timber left the public would have to continue to make long-term investments in

[15] On most public forests there is some timber of little value for sale or as growing stock which could properly be used for homestead construction.

planting, fire protection, and other forestry work. In many areas there are adequate timber resources to expand employment in timber cutting if new markets and new industries can be developed which are adapted to the kinds of second-growth timber available.

A recent estimate places total additional employment needs in the cutover region at 60,000 man-years, including urban as well as rural workers.[16] The full burden of supporting all these people cannot properly be placed on the forest resources of the region, but scientific forest management can ultimately find jobs for many of them. In parts of Europe where intensive forestry is practiced the time of one man is required on each 100 acres. Forestry cannot be practiced on such an intensive scale in the Lake States. But if at present only one man per 1,000 acres could be given full-time work the national forests of the region, which cover nearly 6 million acres, should be able to maintain 12,000 homesteaders on half-time work. If state and county forests (containing over 12 million acres) were also managed on this basis, 24,000 homesteaders would be provided for. There is also no reason why private timber owners could not employ forest homesteaders to advantage. No attempt at an exact forecast is here made, but these figures indicate the potential capacity of the forests of the region to provide productive work.

3. In the long run public forest homesteads should be conducted on a self-liquidating basis. Cash income would be derived primarily from timber and other forest products. It is clear that, when the forests are in production, the homesteaders are going to be badly needed for protection and improvement work and for timber cutting.

The immediate costs of this program would depend on how rapidly it is put into operation. The heaviest expense would be incurred during the first few years in supervising homestead development and, when jobs are scarce, in providing employment on conservation projects. It would certainly not cost any more to establish and maintain a family on a forest homestead than it does to hire, equip, and supervise one Civilian Conservation Corps boy. Many of these families are receiving relief money anyway, and so the cost would not be any greater if they were employed on forestry work, in which there is some prospect of liquidating the investment.

[16] Peterson, Lyall, "A Permanent Solution to Unemployment and Relief Problems in the Northern States through Forestry Measures." July, 1940. Unpublished manuscript.

4. The resettlement and reëmployment program on the Chippewa National Forest has shown that little new federal authorization would be needed to carry out a similar plan on a broader basis. There is already available within the Department of Agriculture most of the machinery for land exchange, farm-improvement loans, free-use (timber) permits, sales of timber at cost, small timber sales, and so on. Past advances have been limited by lack of a clear-cut program and the personnel to push it. However, a federal forest homestead act which would establish an active policy toward local settlers and clarify the authority of forest officers would serve a useful purpose. The states and counties need not only policy-forming legislation, but also additional funds and personnel if their forests are to be placed under constructive management for the benefit of the local people.

5. The Drummond project in Wisconsin has proved that the rehabilitation of forest workers cannot be entirely successful unless it is done as part of a larger scheme to develop the forest resources and timber markets to their full capacity. Thus a supplemental program would be vital to the success of the public forest homestead plan. Such a program should include the following elements:[17]

(*a*) Encouragement of coöperative logging, milling, and marketing of forest products in order to increase the efficiency and bargaining power of small logging and milling operations which have been so prevalent in the Lake States in recent years.

(*b*) Government logging should be authorized where mature and overmature timber is available, but sales of stumpage are not bringing the volume and stability of employment needed by local woodsmen. This is not so radical a thing as might at first appear. In Europe the harvesting process has always been considered simply a phase of the job of growing timber, just as the farmer considers harvesting a part of his job. That government-logged timber would glut the lumber market need not be feared if it goes into construction of forest homesteads, into new industries, and into low-cost housing according to the plans outlined under (*c*) and (*d*) below.

(*c*) New industries capable of using low-grade second-growth timber should be encouraged by research, low-interest loans, and gov-

[17] White, H. G., "How Forestry Can Help to Solve the Unemployment Problem." Statement prepared for Congressional Committee on Unemployment, Seventy-sixth Congress.

ernment pilot plants. As more and more big sawmills close down owing to exhaustion of old-growth timber and inability to operate on smaller timber there are going to be real opportunities for the development of new industries.

(*d*) During recent years both urban and rural home construction and repairs have lagged far behind normal requirements. This means that many people are living in unsanitary tenements, obsolete homes, and flimsy shacks. The construction industry, even with present federal assistance, has failed to tap this huge market for low-rent and low-cost houses.[18] Most low-income groups have idle time which could be put into home construction. A self-help housing program for both farmers and city dwellers is needed to meet this situation.

(*e*) In the long run, everything which builds up the forest resources and leads toward sustained-yield management of private timber holdings will increase the volume and stability of employment. For this reason every effort should be made to extend public ownership and control over as much as possible of the private timberlands that are not being properly managed. Public regulation of cutting practices should also be adopted in order to prevent continuation of destructive logging and, consequently, the further aggravation of the problem of idle forest land and idle woods workers. Those private land owners who have demonstrated their willingness and ability to manage their timber on a permanent basis should be given every encouragement. But if they require such large public subsidies that the Government has to put in as much money as would be required to buy the land, the land might as well be placed under Government ownership in the beginning, so that the public interest will be fully protected.

One should be suspicious of any simple panacea prescribed for the complex social and economic ills of a cutover region such as the Lake States. The establishment of public forest homesteads alone will not be enough. But if the problems of the region are attacked concurrently along all the fronts indicated above there is hopeful prospect for development of a stable and prosperous forest economy. The attack must be integrated. It must be centered on immediate

[18] *Investigation of Concentration of Economic Power. Part XI, Construction Industry.* Hearings before Temporary National Economic Committee, Seventy-sixth Congress. Washington: Government Printing Office, 1940.

needs. The public forest homestead plan supplies that unified approach, for it reduces the problems of the people to two basic elements — the need for a home and the need for forest land from which to earn a permanent livelihood. The plan, then, seeks directly to supply those missing elements.

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